THE GUNONG BENOM EXPEDITION 1967

11. NOTES ON ZOOGEOGRAPHY, CONVERGENT EVOLUTION AND TAXONOMY OF FLEAS (SIPHONAPTERA), BASED ON COLLECTIONS FROM GUNONG BENOM AND ELSEWHERE IN SOUTH-EAST ASIA

1. NEW TAXA (PYGIOPSYLLIDAE, PYGIOPSYLLINAE)

By ROBERT TRAUB

CONTENTS

SYNOPSIS

Stivalius robinsoni (Rothschild, 1905) and its allies constitute the dominant group of fleas infesting squirrels and tupaiids in the forested foothills of much of the "Indo-Malaysian" region ranging from Indo-China (and perhaps eastern India) through Malaya, to Indonesia and the Philippines. The taxon is reviewed and a new genus is proposed and named to encompass the 4 previously known species and 9 new species. Descriptions, diagnoses and detailed illustrations are provided for these 13 species and 4 new subspecies. The members of the *Stivalius ferinus*-group are also discussed and placed in a separate genus, which is named, described and illustrated, along with a new species from North Borneo and some of the species heretofore known. For purposes of comparison, *Stivalius* Jordan & Rothschild, 1922 *s. str.* is redescribed and figured, and a new subspecies of *S. cognatus* Jordan & Rothschild, 1922 is used to illustrate the diagnostic features of the generic level and those for species and subspecies. Notes on the host-relationships and distribution of these fleas are presented, as applicable. Keys to the known species and subspecies are included for all the genera treated.

INTRODUCTION

The genus *Stivalius* Jordan & Rothschild, 1922 (*s. lat.*) includes some of the most prevalent and characteristic fleas parasitizing rats, squirrels, tupaiids or other small mammals over much of southeastern Asia and the Indo-Australian Archipelago, and hence throughout this vast area *Stivalius s. lat.* must be considered as of potential importance regarding vectorship of any infection harbored by rodents and other such mammals. In fact, species of *Stivalius* have been found infected with plague in India and Java (Pollitzer, 1954), as is pointed out below.

The fleas collected by Lord Medway's team on Gunong Benom in Pahang, Malaya (W. Malaysia) amply indicate the predominance of *Stivalius s. lat.* in the relatively untouched dipterocarp forests of that country, but the value of the collection far exceeds that point, or that of the new species represented therein. The specimens

well illustrate certain major points concerning the systematics, zoogeography and evolution of fleas, and contribute to our understanding of the current and past distribution of host-mammals. The findings emphasized the need for the revision of the classification of the *Stivalius robinsoni*-group of fleas, and of certain other members of *Stivalius s. lat.*

For these reasons, it was decided to regard the Medway collections as the foundation and catalyst for a study dealing successively, in three articles, with taxonomy, convergent evolution and zoogeography of certain groups of *Stivalius*. This first paper in the series includes: (1) the erection of a new genus for the *S. robinsoni*-group, with descriptions and illustrations of nine new species and four new subspecies, along with keys for the identification of the 13 known species and four subspecies. The hitherto unknown female of *S. loncha* Jordan, 1926 is described. (2) A discussion of the hosts and distribution of the Malayan peninsular species of the *S. robinsoni*-group. (3) A new genus for the *S. ferinus*-group, with descriptions and figures of one new species and a key to the five known species. (4) A redefinition of *Stivalius s.str.*, for purposes of comparison with the new genera, and based upon a new subspecies of *S. cognatus* Jordan & Rothschild, 1922, along with keys to the described forms (four species and three subspecies), including the hitherto unknown male of *S. c. spiramus* Jordan, 1926. Dorsal or ventral views of the aedeagus are presented to elucidate some of the major points in systematics, comparative morphology or convergent evolution.

The second and third articles in the series follow immediately after this one.

MATERIALS AND METHODS

Methods of Collection and Handling

It is emphasized that throughout the course of the field-projects in Malaya, Borneo, Thailand and other countries, which resulted in the specimens treated in this article, the collectors were primarily engaged in other types of studies. The investigators were actually working on scrub typhus, leptospirosis and other infections, or doing research on land-leeches, or engaged in malaria-control, or conducting survey-type operations, and the small number of specimens of fleas obtained at times, and the limitations of the data on infection-rates, reflect the necessarily secondary nature of the collecting-programs.

The bulk of the specimens were collected by the writer while serving as Commanding Officer of the U.S. Army Medical Research Unit (Malaya) during varying periods in Malaya from 1948 to 1959, or by teams of the Colonial Office Medical Research Unit (later Division of Virus Research and Medical Zoology) of the Institute for Medical Research, under the direction of Dr J. R. Audy. Both of these Units were based on the grounds of the Institute for Medical Research (I.M.R.) at Kuala Lumpur and worked closely together. Other important collections were made by the Department of Zoology, University of Malaya (UM), by teams led by Lord Medway or J. R. Bullock. The U.S. Army Medical Research Unit (USAMRU) required live animals for its research on infections, while the British (later Malaysian) Unit (henceforth indicated as DMZ-IMR) was collecting living animals in connection with studies on

ecology. Lord Medway also frequently needed the animals alive for his investigations.

For these reasons the vast majority of rats, tree-shrews and ground-squirrels, and even many tree-squirrels, examined for fleas in Malaya had been trapped in various types of live-traps, predominantly in the "wire basket-trap," a modification of a trap of presumed Chinese origin and commonly used for catching rats throughout southeastern Asia. In this type of device, constructed of thin chicken-wire, the front door is closed by a spring when the mammal tugs at the bait on a hook and thereby releases the mechanism holding the door open. A folding-trap of heavy wire, of U.S. design, was also employed and in this type, the door was released by a treadle on the floor. Closed traps of galvanized metal, operating in a similar way, were also used. Another kind was prepared by fastening a large can to an ordinary large snap-trap and placing a screen on the movable arm of the trap. When released, the arm would hurl the rat into the can and close the aperture.

Sundry modifications of these and other live-traps were employed, but regardless of the model, there were always inherent disadvantages insofar as concerns the collecting of fleas. Certain species tend to leave the host soon after feeding to repletion, others do so when the animal becomes excited, and its fur gets ruffled, as happens when the mammal realizes it is trapped. Since the traps were generally examined but once daily (and the animals became agitated anew at the approach of the collector), many fleas were undoubtedly lost before the host could be popped into a cloth bag for subsequent examination. In traps made of mesh, the mammals would become drenched during showers of heavy rain, which usually are a daily occurrence in or near the tropical rain-forests. In traps of solid metal, the host often became too hot, and hyperactive, or died as a result, while at other times, as at night, they became wet and cold with equally disastrous results. These consequences all affected the degree of flea-infestation at the time of collection, as did the attack on the hosts by myriads of ants, both large and small, which was a fairly frequent occurrence.

On the other hand, utilization of traps which killed the victims, i.e., snap-traps of sundry sizes, or dead-falls, had other and more serious disadvantages, even though some species of fleas linger for hours on a dead host. Within minutes, dead rats almost invariably attracted swarms of ants, whose movements through the fur unquestionably hastened the departure of many fleas. The removal of innumerable chunks of skin by the ants also would effectively depilate the carcass within an hour or two, and only exceedingly rarely was a flea ever noted on the body of an animal infested by ants. Even when the traps were examined every hour it was impossible to cope with the depredations of the ants in some areas. Nevertheless, the use of snap-traps was a useful adjunct, especially in the mountains, and certain "rare" fleas were collected by this means.

The bait used in the trapping operations consisted of fruit such as bananas or durian, burnt coconut, nuts, peanut butter, sweet potato or other yams, dried fish, bacon, a mixture of oatmeal, peanut butter and bacon, etc. Baits that were sweet (e.g., raisins) or oily or fat tended to attract so many ants that they were soon eaten without trace.

Trapping was supplemented by shooting, and most of the tree-squirrels and some of the ground-squirrels and *Tupaia* were collected in this way. Carnivores, in particular, were taken by shooting, usually at night, when their eyes would glow in the light from powerful flashlights.

All hosts, including live animals, were immediately placed in individual cloth bags on collection and the bags were sealed pending examination in the laboratory. The bags of dead specimens were treated with chloroform and sprayed with aerosol insecticide to stupefy or kill the fleas; while live animals destined for release after checking were exposed to ether long enough for anesthesia, whereas those required for microbiological study were chloroformed. (Chloroform is more effective but ether is less toxic, hence the use of the latter.) If living chiggers or other ectoparasites were required for inoculation, rearing or study, the host was asphyxiated after exposure to the anesthetic; the host was then brushed vigorously while it was held over a tray, and the stupefied fleas which fell in the process were collected via forceps and preserved in 70% ethyl alcohol. The brushing was repeated several times because of the difficulty in collecting all the fleas hidden in the fur. The fleas were prepared for definitive examination and study by placing them in 10% KOH for 24–48 hours or until the internal tissues had dissolved, after which they were washed in water, dehydrated by exposure to 70%, 95% and 100% ethyl alcohol in series, cleared in oil of wintergreen and mounted in Canada balsam on microscope-slides.

In the case of mammals collected by USAMRU, records were kept as to the numbers of hosts which were not infested with fleas. This was not possible routinely for the collections by our colleagues, but the difficulties mentioned above in collecting fleas in the tropics serve to demonstrate inherent limitations in obtaining infestation-rates in such regions. When discussing the numbers of fleas taken from various hosts, as in Table 2 (p. 259), the entry "minimum number exam'd." therefore refers only to the mammals collected by USAMRU.

Major Collection Areas

Specimens of fleas of the *S. robinsoni*-group were never taken in fields of grass or waste land, but only where there was forest, at least in remnant form. Accordingly, the major collecting areas on the Malayan peninsula were in the dipterocarp forest in the lowland or foothills, particularly within 20 miles of Kuala Lumpur, i.e., the Forest Reserves at Gombak, Ulu Langat, Bukit Lagong and Kepong, and also at Klang Gates (Selangor), where trees such as *Shorea*, *Dipterocarpus*, *Swintonia* and *Balanocarpus* and *Hopea* dominate the forest. Most of the collections were made between 800 and 2000 ft elevation (mainly at 1500 ft) in areas which were still largely "primary jungle" in 1948–49 but which were thereafter fairly extensively but selectively thinned for timber so that by 1956, bamboos and other features of secondary forest were evident in scattered patches throughout. The findings in the dipterocarp forest are treated below as "Kuala Lumpur Forest" (Table 1, p. 216, et seq.). Another well studied site was the Subang Forest Reserve west of Kuala Lumpur, about 8 miles from Batu Tiga on the Batu Tiga–Subang road. Here the forest was of a much more secondary nature and at a lower elevation (at about 200–600 ft) than in the wooded habitats mentioned above.

Field work was undertaken in the limestone hills west of Ipoh, Perak, as a result of an outbreak of scrub typhus in British forces operating deep in the (secondary) forest. This was in the Kledan Saiong Forest Reserve, 8 miles west of Ipoh and again 10 miles northwest of Ipoh, each trip including about 4–5 days intensive collection at elevations of about 800–1100 ft in September–October 1958. The habitat at Gunong Benom, the scene of operations for Lord Medway's expedition, has been discussed elsewhere in this volume. Limited collections were also made by USAMRU in the coastal or adjacent forests of the East Coast, i.e., at Kuantan, Pahang, and at Bukit Besei in Trengganu. Another area of dense lowland forest briefly examined was that in Kelantan.

Over the years, about one month was spent by USAMRU (and an equivalent period by DMZ-IMR) collecting in the montane forests in the vicinity of Fraser's Hill (3500–4500 ft elev.), the Cameron Highlands (4500–6600 ft), and about 2–3 weeks at Maxwell's Hill (3900–4200 ft) and Kedah Peak (Gunong Hijau, G. Jerai) (3500–3900 ft). These areas, in general, have essentially the same mammalian, siphonapteran and trombiculid fauna and hence the collections are consolidated under the caption "Mountains" in the discussion of host-relationships below (but an exception is noted in the case of Kedah Peak). An interesting set of specimens was taken in Kedah by a group from the Department of Zoology of the University of Malaya (UM) under the direction of J. R. Bullock. This was at the Bukit Wang Forest Reserve at Jibra and the results are treated separately. Other valuable material was collected by UM teams on Tioman Island (Pulau Tioman) off the East Coast of Malaga.

Although three joint teams of USAMRU and DMZ-IMR operated on Mt. Kinabalu, North Borneo (Sabah), based at 5000 ft elevation at Tenompak for periods of about 4–6 weeks annually, in 1951–1953, and Lord Medway's group also collected there subsequently, as have other naturalists interested in ectoparasites, no specimens of the *S. robinsoni*-group have ever been taken at such altitudes (or higher) in Borneo. However, we did find such fleas on flying-squirrels and in squirrel nests, etc., in the vicinity of Ranau, at the base of this mountain, as indicated in the description of a new species below.

Other areas where members of the *S. robinsoni*-group were taken, in Sarawak, Thailand and Indonesia, etc., are indicated, along with the collectors, in the descriptions that follow. The individuals and institutions participating in all of these studies are mentioned in the paragraph on acknowledgements.

Introductory Remarks Concerning the Descriptions

Format and Keys

The *S. robinsoni*-complex of fleas is relatively rich in numbers of species, and some of these are superficially similar in appearance (although differing abundantly in critical details—at least in the males). Moreover, as many as three species have been collected on the same individual ground-squirrel. Accordingly, in order to facilitate identification and to provide an adequate background for the evaluation of differences at the generic-, species- and subspecies-levels and for use in discussions on evolution and zoogeography, the various species are diagnosed and illustrated in detail.

Further, the first new species is described in full so as to serve as the basis for comparison for the forms that follow. Major distinctions alone are therefore stressed in diagnoses, and only significant morphological differences are cited in the descriptions following such analyses. In the keys for identification of species and subspecies, frequently more than one set of diagnostic characters is cited in the couplets. This was done to facilitate the use of the keys, so that if there is indecision about one point, an alternate is available. It is stressed that each feature is diagnostic, i.e., only one need apply, and hence the couplets do not deal with combination of characters, but with alternates.

Landmarks and Points of Reference Used in Taxonomy

The most important features for classifying the members of the *S. robinsoni*-group (and other *Stivalius s. lat.*) are in the male sternum 9 and the aedeagus, and in the internal genitalia of the female, including characters unused or un-noted in the past. These are all labeled and indicated in the text and figured and defined, if new. However, in addition there are morphological structures and "landmarks" that are useful in taxonomy but which are difficult to describe in a few words, or to locate precisely because they are on a curved surface, or else are not oriented in the usual fashion (i.e., the "ventral arm" of the male sternum 9 is often caudal or vertical in position).

For clarification and simplification, therefore, a system of reference-points, utilizing lower case letters, has been employed in some instances (head, claspers, male sternum 8 and sternum 9) to designate the specific level or site being described or compared.

Claspers, Sterna 8 *and* 9. The need for a system of this type becomes apparent by a glance at figs 28 and 29, the male sterna 8 (8 S.) of two allied fleas. It is obvious that the outlines of the sterna differ markedly, and in the case of the former (fig. 28) the temptation is to say the "dorsal margin is flattened." However, a question arises as to the "dorsal margin" in the latter, for what appear to be the anterior and posterior margins curve together imperceptibly. Moreover, study of the cutaneous marking or striae indicates that the dorsal margin really extends down to the first (uppermost) large bristle on the caudal margin.

The structure herein termed the "lumacaudate process" (LUM.), on 8 S., emphasizes the problem, for while there are noteworthy differences in proportion, there are inadequate landmarks to use in comparison. Thus, in the case of fig. 29, the length is fairly easy to determine because the dorsal margin is outlined, but this is not so in the other species.

Accordingly, the following reference-points have been selected as guide-marks. In the case of the claspers and sternum 9, they are illustrated only in figs 1 and 3 which were specially prepared for this purpose, although the abbreviations are frequently used in the text. It will therefore be necessary to refer to these figures, or to the List of Abbreviations (Landmarks and Points of Reference on p. 298) below, in order to properly utilize this system. However, the text has been so prepared that the sundry structures are generally described in the usual manner and hence are self-explanatory, while the reference-points are cited to serve as supplemental guides.

The exceptions are instances used in comparisons, and these immediately follow such descriptive phrases, and therefore should not be confusing.

Chaetotaxy and Dimensions of the Preantennal Region. Members of *Stivalius s. lat.* are liberally endowed with bristles, and the number and shape of the sundry preantennal bristles are often important in taxonomy. Unfortunately, the bristles (except for those in the first row) are usually not arranged in definite rows, unlike some other groups of fleas. Moreover, when relatively large numbers are present, there is some variation in both arrangement and actual number, in accordance with a well known principle in insects. In order to facilitate discussion and indication of the major preantennal bristles, an arbitrary system has been used to designate "rows" of bristles, as shown in fig. 2 (I–IV). No logical pattern could be discerned which would encompass all the large bristles, and the one or more which do not fall in the rowa are indicated as "supernumerary" (SY.). It should be noted that not all the members of "*Stivalius*" have preantennal chaetotaxy that jibes with even this arbitrary system, but at least it is possible in this way to more readily categorize and denote the "exceptions."

In the species illustrated in fig. 2, the bases of the anteriormost row of bristles are linked by a cuticular line and hence this row, designated as I, is unmistakable. The next row, of four subvertical large bristles, is II. The third row, III, distinguished by the eye-bristle (E.B.), which is above and anterior to eye, may be termed the eye-row (E.R.B.). It consists of three sub-horizontal long bristles, and commences in line with the ventralmost of II. Row IV is likewise sub-horizontal and is termed the genal row of bristles (G.R.B.), ranging along ventral margin, from the base of the maxillary lobe (MX.) half-way towards the ventral part of the eye. In addition there is one large bristle out of line, between II and III; it is designated as a supernumerary (SY.).

The shape of the head is likewise of significance in the classification of pygiopsyllids, but here, too, difficulties arise. Not only do the sexes differ (as in other fleas), and there also are the usual problems of indicating unmarked points on curved surfaces, but variations occur in the position of certain "landmarks," depending upon the taxon. Thus, in one new genus herein described, the maximum length of the preantennal region is at the level of the median sensillary crater (fig. 2, M.S.C.), but in another, the crater is more dorsal in position, where the frons is narrower. In some instances the labral or anteroventral angle of the head is in line with eye-bristle, in others, not. Those "lengths" are therefore not comparable. Another problem is that structures that would appear to be useful as landmarks are either movable, and hence subject to individual variability (i.e., the palpi and the maxillary lobe), while others are at times impossible to see clearly (i.e., the bases of the palpi). In order to make valid comparisons, therefore, guide-marks are indicated in fig. 2 as follows:

The *height* of the preantennal regions is measured from the level of the vertex at the falx, viz., j3–i3, to the true ventral margin of the head (f4–g4). The *length* may be measured at various levels, according to genus and sex, but always should be along lines parallel to the longitudinal axis of the flea, and directed to the margin of the antennal groove, i.e.: (1) immediately below the middle sensory crater (M.S.C.)

(x3–y3); (2) the dorsalmost long bristle of row I (z3–a4); (3) *ibid.* for row II (a4–b4); (4) the eye-bristle, which at times is in line with the labral angle and then would be d4–e4; and (5) the most anterior point on the arc of the frontal margin, which in fig. 2 is the same as level b4–c4. Other aspects of this system are cited in the List of Landmarks (p. 298).

A. **Medwayella** gen. nov.

Diagnosis. ♂ instantly recognizable by the ventral spinose "lumacaudate" process on sternum 8 (figs 29, 12, LUM.). Shape and structure of ♂ sternum 9 (figs 1, 18, 20) and of sclerites of aedeagal endchamber (figs 10, 22–25) are characteristic and are described below. Spermatheca (fig. 15, SP.) shaped somewhat like a ground-nut or peanut and with basal portion of duct of spermatheca (figs 15, 27, D.SP.) bearing internal sclerotized rings. ♀ basal sternum with lateral patch of bristles restricted to proximal portion of segment. ♀ tergum 8 bearing a mesal tanned zone (figs 27, 31, M.R.8) anteriorly marked by a vertical ridge and a contiguous dark ovoid area.

Generic Description. Caput integrecipit (figs 4, ♂; 6, ♀). Anterior margin of head evenly ovate, upper half more rounded than lower. Front part of ♂ head about thrice as high (from vertex at falx, to ventral margin) as long (at level of dorsalmost bristle of row II, viz., b4–c4 in fig. 2). Preantennal region with 4 irregular rows of bristles, the lowest ventromarginal. Eye reniform, well developed, inserted far back, above base of procoxa. Antennal segment 2 with bristles short in both sexes. Antennal groove not extending on to propleuron. Postantennal region with 3 complete rows of bristles. Labial palp (L.P.) 5-segmented (excluding palpiger) and generally reaching near apex of procoxa; occasionally longer (fig. 104).

Prosternosome lacking distinct sinus for receiving first vinculum (VC.1.). Dorsal margin of pronotum subequal to, or slightly longer than, length of adjacent spines of comb. Mesonotum (fig. 9, MSN.) generally with 1 pseudoseta (PS.S.); subdorsal. Pleural arch (figs 6, 9, PL.A.) well developed. Metanotum (MTN.) lacking apical spinelets. Metacoxa lacking mesal spiniforms, but with a few mesal thin bristles. Profemur lacking a group of mesal bristles but with scattered lateral ones. Meso- and metafemora lacking median and submedian lateral bristles. Dorsolateral bristles in notches on posterior (outer) margin of tibiae largely paired. First metatarsal segment about 1·6 times length of II and nearly 2·5 times that of mesotarsus I. Third metatarsal segment longer than fifth. Except for fringe on first segment of protarsus, none of tarsal bristles extending well beyond middle of following segment. Tarsal segment V with 6 pairs of stout lateral plantar bristles, of which first pair displaced towards midline on pro- and mesotarsi (fig. 7), and third pair somewhat so displaced on all legs (fig. 8, metatarsus). Fourth vinculum (fig. 9, VC.4) usually upright and not projecting forward as a short rod. Some abdominal terga with 1 subdorsal apical spinelet. Unmodified terga very broad, extending ventrad to lower third or fourth of sterna; with 2 virtually complete rows of bristles in ♂, 3 in ♀ but incomplete. Basal abdominal sternum of ♀ with lateral patch of small bristles, but these near anterior margin; nude in ♂. Fossae of representative abdominal spiracles sagittate. Both sexes with 2 antepygidial bristles per side (figs. 11, ♂;

26, ♀, A.B.). Tergum 7 of ♀ with some bristles modified to resemble antepygidials, i.e., 1 dorsomarginal (U.M.B.), one immediately below plate of A.B. (L.M.B.) and 1 (L.B.M.-2) in ventrocaudal corner of group of bristles of 7 T. Tergum 7 produced into a short lobe (U.L.7) above A.B. plate and, in ♀, a longer, pointed lobe (L.L.7) immediately below it. Sensilium (pygidium) higher than long in ♂ (figs 11, 13, SN.); not as arched in ♀, where dorsal-ventral axis slightly exceeds anterior-posterior axis (fig. 26, SN.).

Male. Tergum 8 (fig. 11, 8 T.) very small, extending only slightly ventrocaudad of its spiracular fossa (8 SPC.). Sternum 8 (8 S. and fig. 28) correspondingly very large, extending dorsad to near base of ventral anal lobe (V.A.L.) and cephalad to about level of A.B.; "lumacaudate" in bearing a conspicuous, spinose, mesal ventral bulbous process (LUM. and fig. 12) arising near middle of ventral margin. "Lumacaudate process" attached to 8 S. by an apical fold or seam (S.LUM.); inner surface armed with close-set spiniforms from near basal fourth or fifth, to apex; spiniforms directed mesad. Ventral anal lobe (fig. 13, V.A.L.) with ventral margin with a conical process at middle; this bearing 1 long apical bristle, hence structure somewhat resembling anal stylet of ♀ (fig. 27, A.S.). Subanal sclerite (S.S.) relatively large and well tanned. Manubrium (MB.) broad to near apex; ventral margin with apical third quite straight but usually biconvex near middle; dorsal margin somewhat convex; its bay (B.MB.) extending cephalad to near apex. Immovable process of clasper (figs 14, 17, P.) dorsally somewhat truncate except for caudomarginal bulge around longish apical bristle; with a smaller dorsal bristle. Conical process (C.P.) of P. usually more than 5 times as long (cf. fig. 1, e–h)[1] as broad at middle (f–g). Movable finger (F.) of clasper with stiva (STV.) (distocaudal extension) too short to resemble a plough-handle and base far too broad to look like a plough-shaft (in contrast to the condition in *Stivalius s. str.*, which suggested to Jordan the coining of the generic name based upon the Latin word, *stiva*, for plough-handle). Caudal margin of F. usually sigmoid so that F. is narrowed subapically and bulges caudad proximally. Distal fringe (D.FR.) generally of about 4 stout bristles; subapical, at level of sensilla-group (S.G.) of 3 short bristles; the bases of bristles of the fringe mesal and slightly anterior to caudal margin of F. (vide fig. 87). Fulcral sclerite (F.S. and fig. 65) of F. about 1·3 times as long (high) (fig. 1, ww/xx–zz/a3) as broad at expanded base (ww–xx). Tergal apodeme of segment 9 (T.A.P.9) long and narrow. Proximal arm of sternum 9 (P.A.9 and fig. 63) apically massive, and base rapidly broadening so that subapical breadth (cc–ee) is about 2·5 times that of base (gg–hh).

Distal arm of sternum 9 (figs 18, 20, D.A.9) subequal to P.A.9 in length (fig. 1, ii–qq; ii–arc aa/bb) and characterized as follows: (1) Fairly long and narrow, somewhat broadening at level of transverse sclerotization (T.S.) which represents dorsal limit of internal fusion of the two distal arms. (2) With subapical group of 4–6 caudomarginal (ventromarginal) short spiniforms (S.G.SPN.). (3) Caudomarginal submedian group of 2–3 stout bristles (CM.G.B.) above T.S. (4) A median dense

[1] For methods used in measurements, see figs 1–3 and text pp. 209-211. The small letters indicate the points in question; letters connected by a dash denote the two points or axes being measured, while a fraction signifies an imaginary line connecting those points. Thus, ww/xx–zz denotes the distance between zz and an imaginary line connecting ww and xx.

group of microspinules in clear area near tip of D.A. 9 herein termed the subapical patch of microspinules (MSP.P.) and presumably sensory in function. (5) With subapical lobate extension (SUB.L.) on anterior (dorsal) margin; this bearing a group of fine bristles near margin. (6) Often with a distinct subapical dorsal (anterior) notch (fig. 20, NCH.) or broad sinus (fig. 33, ARC.) resulting in a characteristic apical lobe (AP.L.). If sinus or arc absent, then margin between apex and SUB.L. quite homolate ("uniform-sided," viz., flat and unmodified) (fig. 67, HOM.). (7) With a laterad-directed, lightly tanned, flap herein termed the supramedial flap (SUP.FL.) overlapping more mesal patch of microspinules (MSP.P.); its basal margin extending from near level of SUB.L. to, or near, apex of D.A.9, its ventral (caudal) margin delineated by a median arc of thin bristles, the supramedial group (SUP.G.). Base of SUP.FL. associated with a sclerotized thickening (THK.), at least for upper portion. (SUP.FL. appressed to surface of D.A.9 in mounted specimens and hence appearing as contiguous with it and not at all flap-like.) (8) With a convex semimembranous microtufted or microspiculose area in a cavity of anterior (dorsal) margin at level of T.S. herein named the mid-microspiculate area (M.MSP.), and of presumed sensory function. (9) In some species, heavily sclerotized and ventral margin appearing as an apical spur-like extension (fig. 111, EXT.9) because of semimembranous nature of distal portion of dorsal margin.

Aedeagal apodeme (fig. 10, AE.A.) resembling manubrium (MB.) for most of its length; lacking apical appendage. Middle lamina (M.LAM.) with its bay (B.M.L.) extending nearly as far cephalad as anterior margin of bay of manubrium (B.MB.) when the two apices are contiguous. With an ovoid, subdorsal cavity in lateral laminae containing a spiculose body, the entire structure herein termed the caverna spiculosa (fig. 22, CAV.SPIC.). Aedeagal pouch (AE.P.) well tanned; thickened ventral walls (figs 23, 42, AE.P.-V.) extending cephalad to level of F.S. and distad to level of base of sclerotized inner tube (S.I.T.), near base of phylax (PHY.); lateral walls (AE.P.-L.) continuing along sides of the crochet process (CR.P.) and blending with it, appearing at least as the basal ventral portion of the "crochet" (fig. 22) and at times as the entire ventral part (fig. 71); the unified structure, whose components are at times difficult to delimit, herein termed the quasi-crochet (Q.C.). Hood (HD.) sinuate to ventral margin and then projecting anterodorsad as the lateral "deltoid flap" (DEL.FL.), which covers much of the endchamber except for base of phylax (PHY.) and base of S.I.T. Deltoid flap dorsocaudally terminating at dorsal apex of body of crochet (B.CR.); its own apex subdorsal, at level of aedeagal fulcrum (AE.F.). Lateral lobes (L.L.) reduced; primarily ventral in position and mesad of DEL.FL.; extending from apex of thickened ventral margin of pouch wall over base of phylax of crochet process and here merging with caudolateral region of pouch wall (AE.P.-L.). Sclerotized inner tube (S.I.T.) relatively unmodified, fairly long, horizontal and sinuate and with ventral margin extending somewhat more distad than dorsal margin; distal third ridged, often with a dorsal spur-like projection (figs 23, 96). Ford's sclerite (F.SC.) (formerly termed apicomedian sclerite) very well developed; apex of its alpha-portion (ALPH.) thumb-like (THM.) or else forming a groove-like structure (figs 71, 115, GRV.) by paralleling part of the thickened basal margin of the securifer (SEC.). Upper arm (U.A.) of securifer narrowed distally; lower arm (L.A.) broad to

at least middle and then narrowing somewhat. Ford's sclerite bifid to midline in dorsal or ventral aspect (figs 24, 25). Phylax (PHY.) relatively broad (lateral aspect); about twice as high as broad at base; subligulate, with ventral margin straight; arising near apex of pouch wall at fusion with lateral lobe (L.L.) and extending to apex of pivotal ridge (PIV.R.) of aedeagus. With a short, tanned "pivotal chord" (PIV.CD.) linking apicocaudal angle of PHY. with base of U.A., arising at apex of PIV.R. Crochet boomerang-shaped, its body or basal sclerite (B.CR.) vertical, narrow except for expanded truncate apex which is contiguous with base of Ford's sclerite (F.SC.) and junction with DEL.FL.; crochet process (CR.P.) extending caudad as a horizontal digitoid arm and ventrally indistinguishably fused with AE.P.-L. to form the quasi-crochet (Q.C.). Often with a semimembranous spiculose lobe (fig. 22, SPIC.L.) (which is probably the ventral lamella of Hopkins & Rothschild 1966), apparently arising from base of phylax and intimately associated with ventral region of Q.C. Aedeagal fulcrum (AE.F.) quite narrow. Crescent sclerite (C.S.) long. Satellite sclerite (SAT.S.) very short. Central sclerite (CEN.S.) very close to fulcral medial lobe (FUL.M.L.), the two together resembling upper portion of an arrow-head. Lateral shafts of capsule (L.S.C.) well tanned. Y-sclerite (Y.S.) large. Vesicle (V.) well developed. Penis rods (P.R.) short and thick. Third apodemal rod (AP.R.) of endophallus nearly as long and stout as penis rods.

Female. Spermatheca (fig. 27, SP., and fig. 15) with bulga (B.) about twice as long as broad, medially somewhat constricted dorsally and with basal (caudal) part of bulga slightly broader than apical; hilla (H.) short, basal portion internal and entire length only slightly exceeding maximum girth of bulga; with an apical papilla (PAP.). Duct of spermatheca (D.SP.) with portion near bursa copulatrix greatly dilated (figs 27, 77, DIL.P.) and with long internal slightly sclerotized annulae; middle portion narrower and bearing a ladder-like series of internal sclerotic rings; portion nearest spermatheca still narrower and also with dark annulae. Blind duct of bursa copulatrix inapparent. Bursa copulatrix (B.C.) with its perula (P.B.C.) somewhat ovate (fig. 31) or broadly vermiform (fig. 77). With a large sac (SAC.) associated with DIL.P. and dorsal region of perula. Duct of bursa copulatrix (D.B.C.) lightly tanned and sinuate (degree depending upon relative position). Lura of bursa copulatrix not specialized. With an accessory "gland"[2] or fissure anterior to glandula vaginalis (G.VG.) and at times, one caudad. With a paired, internal, semimembranous structure lying between bursa copulatrix and ventral part of sternum 9 (9 S.), immediately above G.VG. and caudoventrally associated with dorsal wall of vagina at genital chamber, and herein termed the paragenital morion (PG.M.). When well developed, PG.M. occupies most of this space (i.e., fig. 77) but it may be greatly reduced (fig. 31). It is of unknown homology and function but may have something to do with the muscles controlling the vaginal aperture and/or with the bursa copulatrix. Sternum 7 (7 S.) with a ventral lobe. Ventral anal lobe (figs 16, 27, 73, V.A.L.) with base short; apical margin long and sinuate, with spaces between groups of long bristles. Dorsal anal lobe (D.A.L.) with 1 long bristle above, and another imme-

[2] These "glands," like the glandula vaginalis and duplicatura vaginalis, presumably house various hooks or lobes of the male in copulation, and are probably not glands in the usual sense of the word, although they may be lined with cells that provide lubrication, etc.

diately below base of anal stylet (A.S.), which is quite straight, long and narrow. Tergum 8 (fig. 26, 8 T.) with caudal margin bearing a long, shallow sinus extending from near apex to lower fourth; usually with a protruding lobe at ventrocaudal angle; with a pair of mesal, long, thin marginal setae above lobe and another pair of such genitalic bristles at level of V.A.L. With mesal tanned genitalic ridge (M.R. 8) marked by anterior, often sinuate or crescentic, vertical thickening, the dorsal or median portion of which is buttressed by a small ovoid sclerotized area. Eighth spiracular fossa (8 SPC.) relatively small, vertical portion ovate, about twice as high as long. Sternum 8 (figs 27, 32, 8 S.) flask-shaped, with dorsoapical short bristles.

The type of the genus is *M. dryadosa* sp. nov. described and figured below. Here also belong the members of the "*Stivalius robinsoni*-group" of Smit (1958), viz., *robinsoni* (Rothschild, 1905), *rhaebus* Jordan, 1926, *lonchus* Jordan, 1926, *javanus* Jordan, 1933 (to use the original spelling, instead of the feminine endings, as henceforth) and the additional new species described below.

Comment. The genus is named for Lord Medway, both for the present holder of the title and for the former, now the Earl of Cranbrook, in token recognition of the many contributions these scientists have made to the study of the natural history of mammals and birds in the Indo-Malaysian area. It is also pertinent and significant that the Earl of Cranbrook's collections of insectivores in remote regions of northeast Burma and those of his son Gathorne, the current Lord Medway, in Malaya and Borneo, led to the discovery of new and little-known fleas and added considerably to our knowledge of zoogeography. Science is also indebted to these investigators for the encouragement given to other workers to undertake such faunal behavioural and distributional studies.

Additional comments on the genus follow the descriptions of new species below.

1. **Medwayella dryadosa** sp. nov.

Type material. Holotype male (B-45320-1) ex *Rhinosciurus laticaudatus*; MALAYA: Selangor, Gombak Forest Reserve, 16 mi N of Kuala Lumpur; 300 m elev.; Coll. R. Traub for U.S. Army Medical Research Unit (Malaya); 22.VII.1956. Allotype female (B-47809) ex *R. laticaudatus*; MALAYA: Selangor, Ampang Reservoir, Ampang Forest Reserve; 1.V.1958; Coll. R. Traub. The data for 80 ♂ and 51 ♀ paratypes are summarized in Table 1, which cites the hosts and localities represented. Holotype (U.S.N.M. number 71598), allotype and paratypes deposited in the U.S. National Museum, Washington, D.C. Paratypes deposited in the collections of the British Museum (Natural History), Bernice P. Bishop Museum (Honolulu), Field Museum of Natural History (Chicago), the Canadian National Collection (Ottawa), the Division of Medical Zoology, Institute for Medical Research (Kuala Lumpur), the Parasitological Laboratory (Stavropol, Caucasus, USSR), the Rijksmuseum van Natuurlijke Historie (Leiden, The Netherlands), Robert E. Lewis, E. W. Jameson, the author, etc.

Diagnosis. Agrees with *Medwayella robinsoni* in possessing a distinct subapical notch near apex of dorsal (anterior) margin of distal arm of ♂ sternum 9 (figs 20, 21,

Table 1.

Summary of Data for Collections of Paratypes of *MEDWAYELLA DRYADOSA* sp. nov. and *MEDWAYELLA PHANGI PHANGI* sp. nov. in Malaya

Host	Spp. of MED.	1. Kuala Lumpur Forest	2. Subang Forest	3. Ipoh Hills	4. Gunong Benom	5. E. Coast Forest	6. Kelantan Forest	7. Mountains	8 Kedah or Perlis
A. *Callosciurus notatus*	M.D.	–	–	–	–	–	–	–	–
	M.P.	–	1♂ 1♀	–	–		–	–	2♂
B. *Sundasciurus tenuis*	M.D.	–	–	–	–	–	–	–	–
	M.P.	1♂ 1♀	4♂ 11♀	12♂ 7♀	–	–	–	–	–
C. *Tamiops macclellandi*	M.D.	1♂	–	–	–	–	–	–	–
	M.P.	–	–	–	–	–	–	–	–
D. *Tupaia glis*	M.D.	4♂ 4♀	2♀	–	–	1♂	–	1♂ 3♀	1♂ 1♀
	M.P.	1♂	4♂ 5♀	6♂ 1♀	–	–	–	–	13♂ 5♀
E. *Tupaia minor*	M.D.	–	–	–	–	–	–	–	–
	M.P.	–	1♂	–	–	–	–	–	–
F. *Rattus bowersi*	M.D.	–	–	–	–	–	–	1♂	–
	M.P.	–	–	–	–	–	–	–	–
G. *Rattus rajah*	M.D.	3♂ 1♀	–	–	–	–	–	1♀	–
	M.P.	–	–	–	–	–	–	–	–
H. *Rattus muelleri*	M.D.	1♂ 1♀	–	–	–	–	–	–	–
	M.P.	–	–	–	–	–	–	–	–
I. *Rattus tiomanicus jalorensis*	M.D.	–	–	–	–	–	–	–	–
	M.P.	1♂	–	–	–	–	–	–	–
J. *Dremomys rufigenis*	M.D.	–	–	–	–	–	–	2♂	–
	M.P.	–	–	–	–	–	–	–	–
K. *Lariscus insignis*	M.D.	4♂ 3♀	–	5♂ 6♀	–	–	1♂	1♀	–
	M.P.	–	–	4♂ 3♀	–	–	–	–	–
L. *Rhinosciurus laticaudatus*	M.D.	41♂ 21♀	6♂ 4♀	2♂	4♂ 4♀	–	–	–	2♂
	M.P.	4♀	–	–	–	–	–	–	–
M. *Ptilocercus lowi*	M.D.	–	–	–	–	–	–	1♂	–
	M.P.	–	1♂	–	–	–	–	–	–
Totals	M.D.	54♂ 30♀	6♂ 6♀	7♂ 6♀	4♂ 4♀	1♂	1♂	5♂ 5♀	3♂ 1♀
	M.P.	3♂ 5♀	11♂ 17♀	22♂ 11♀	–	–	–	–	15♂ 5♀
Collectors		U.S.A.-M.R.U. I.M.R.	U.S.A.-M.R.U. I.M.R.	U.S.A.-M.R.U. I.M.R.	Lord Medway	U.S.A.-M.R.U.	I.M.R. U.S.A.-M.R.U.	U.S.A.-M.R.U.	U. MALAYA I.M.R.

M.D. = *M. dryadosa* M.P. = *M. p. phangi*

NCH.) and thereby separable from other previously described species in which this arm bears a broad sinus instead of a notch, viz., *M. javana* (fig. 134, ARC.) or else lacks a sinus or notch and instead is merely flattened subapically, viz., *M. loncha* (fig. 127) and *M. rhaeba*. Near *M. robinsoni* but separable as follows: (1) Re distal arm of sternum 9 (fig. 20, *M. dryadosa*; fig. 21, *M. robinsoni*; and cf. fig. 1 for abbreviations of reference points). (a) Apical lobe (fig. 20, AP.L.) (oo–qq) above subapical notch (NCH.) squared or truncate across entire breadth in new species, instead of AP.L. being somewhat rounded dorsally (pp–qq) and usually slightly concave ventrally as in fig. 21 (oo–pp) (AP.L.), or angled (fig. 54). In *M. robinsoni*, even if oo–pp is straight and subvertical, pp–qq is convex (fig. 55). (b) Notch (NCH.) symmetrical, shaped like a rounded "U", instead of lower margin (mm–rr) being more oblique and hence with axis of notch (nn–rr) facing more ventrad, and with lower margin (mm–rr) usually distinctly longer than upper (oo–rr). (c) Transverse sclerotization (T.S.) with lower margin quite straight; not sinuate as in fig. 48 (*M. robinsoni*). (2) Re aedeagus (figs 22, 42, *M. dryadosa*; figs 23, 44, *M. robinsoni*). (a) Thumb-like distal region (THM.) of alpha-portion (ALPH.) of Ford's sclerite (F.SC.) with anterior margin ovate and apex subtruncate; about thrice as long (tall) as broad; whereas in *M. robinsoni* "thumb" (THM.) is more rounded and apex ovate; distal margin about 1·2 times as long as thumb is tall. (b) Lower arm (L.A.) of securifer acuminate subapically, not broad to near apex. (c) Ventral region of phylax (PHY.) scarcely broader than at level near S.I.T. instead of being very much broader. (d) Apex of S.I.T. with ventral margin strongly upcurved and extending well distad of dorsal margin instead of only slightly so. (3) Re ♂ sternum 8. (a) Sternum proportionately taller, viz., only 1·4 times as long (fig. 29, p3–t3) as high (i3–r3) instead of 1·7 times as in *M. robinsoni* (fig. 28). (b) Distance between longest bristle on caudal margin and ventral margin (m3–t3) proportionately greater in *M. dryadosa*, i.e., length of sternum at level of that bristle (l3–m3) only 2·2 times distance m3–t3, whereas in *M. robinsoni* it is 2·7 times. (c) Lumacaudate process (figs 20, 29) (LUM.) relatively shorter and broader and apex less ovate, viz., length (q3–s3) along ventral margin only 1·6–1·8 times height at middle (level n3–o3), instead of 2·8 times. (4) Re sternum 7 of ♀ (7 S.; figs 26, 27, *M. dryadosa*; fig. 49, *M. robinsoni*). (a) Sinus on caudal margin with upper margin sloping at angle of 50° in new species, instead of usually about 30°; an imaginary line connecting lobes of this sinus therefore more than thrice height of ventromarginal lobe below sinus, instead of being subequal. (b) Dorsal margin of sinus sinuate; resulting lower sinus much taller than, but not nearly as long as ventral lobe. This margin evenly convex above sinus in *M. robinsoni*. (c) Dorsal margin of sinus does not parallel ventral margin at all but immediately arches dorsad in new species. In *M. robinsoni* the sinus is really a notch. (d) Dorsal third or fourth of this segment broader than in *M. robinsoni* in that caudal margin here sloping at angle of less than 60° instead of nearly perpendicular. (5) Spermatheca lacking dorsal peak on caudal bulge of bulga (figs 15, 31, B.); in *M. robinsoni*, peak (figs 32, 49, PK.) visible if organ is in proper perspective. (6) Perula of bursa copulatrix (figs 27, 31, P.B.C.) about twice as high as broad instead of three or more times (figs 32, 59, P.B.C.). (7) Mesal tanned genitalic area (figs 26, 31, M.R.8) with ovoid sclerotization near middle of vertical ridge, instead of near upper

limit of vertical ridge (fig. 32). (8) Lacking characteristic pair of tanned chords (representing ventral portion of paragenital morion) found just caudad of apex of glandula vaginalis (G.VG.) in *M. robinsoni* (fig. 32). (9) Lacking sclerotized bead-like thickening(s) representing accessory glands in dorsal wall of apical portion of vagina of *M. robinsoni*.

Description. *Head.* (figs 4, ♂; 6, ♀). Anterior margin evenly curved from vertex to ventral margin, arc making a broad semi-ellipse. Front portion of head of ♂, measured horizontally from level of eye-bristle (E.B.) and labral angle (d4–e4 in fig. 2), and vertically from vertex at falx (v3–w3) to ventral margin (f4–g4) of head, about twice as high as long and thrice as long at level of uppermost bristle of row I (z3–a4); in ♀ the corresponding figures are: twice; 2·4 times. With medium and large preantennal bristles arrangeable in 4 rows (the last 3 arbitrary) as shown in fig. 2 (♂). In ♂ first 2 (I and II) subvertical, of 6 and 4–6 bristles respectively; last 2 (III and IV) almost horizontal. Row III, commencing with eye-bristle (E.B.), and Row IV (genal row, G.R.B.) with 3 bristles. With 1 median "supernumerary" bristle (SY.) between rows II and III. ♀ similar but first (uppermost) and fifth bristles of I small; II with 3–4 bristles and "supernumerary" lacking. Eye well developed, reniform, ventrally excised slightly near middle; about 1·4 times as long as high at ventral third; length of eye subequal to that of third segment of maxillary palpus (M.P.). Genal process unspecialized. Maxillary lobe nearly reaching to apex of second segment of labial palpus (L.P.) and to near middle of ultimate segment of M.P. Labial palpus with apical segment nearly 1·5 times length of fourth (penultimate) and extending to near apex of procoxa. Antennal segment 2 with apical bristles scarcely reaching apex of third joint of club. Postantennal region with 3 rows of bristles arranged 5–5(6)–6 in ♂; in ♀: 5 to 7—5 to 7—5 (6) but with a large gap between bristle near lower corner of occiput and second bristle in row, especially in ♀ where space equals length of remainder of row; with an additional long bristle out of line, near antennal groove, below lower placoid.

Thorax. Pronotum dorsally slightly longer than adjacent spines of comb (in ♀ about 20% longer); with 2 rows of bristles, but first row quite short, generally not reaching middle. Pronotal spines about 20 in number (total); base of comb not reaching to vinculum (VC.2); axis of comb very slightly convex, height of arch at lower fourth; lower ⅔ of spines shallowly concave dorsally and ventral margins paralleling dorsal for proximal half and then narrowing gradually, apices pointed, but at about angle of 45° and thus spines fairly broad to near tip; fourth spine (from bottom) the broadest; about 5·3 times as long as broad at middle; most spines with longitudinal axis somewhat oblique from horizontal, i.e., 4 middle spines, slope about 45° near base. Mesonotum (fig. 9, MSN.) with 6 rows of bristles, including the anteromarginal and submarginal short rows of very small bristles; the rows covering entire length of notum (but flange bare); last row consisting of very long bristles (with tiny intercalaries) and this curving ventrally so that lowest bristle appears in line with penultimate row; last 2 rows terminating near level of overlapping dorsum of mesepisternum (MPS.); second and third rows shorter, and of smaller bristles; with 1 pseudoseta per side and that subdorsal. Mesepisternum (MPS.) with 1 long bristle near ventrocaudal angle and this preceded by an arc of 3 small bristles; with lobe at

cephaloventral corner sinuate. Mesepimere (MPM.) with bristles arranged 2–3–1; last contiguous with spiracular fossa. Metanotum (MTN.) with $3\frac{1}{2}$ rows of bristles, of which the first is the half row represented by 2 or 3 members; second extending just below lucodisc. Third vinculum (VC.3) with dorsal surface quite flat except for apical upcurve to point of articulation; axis almost horizontal. Lateral metanotal area (L.M. and fig. 5) with external measurements longer than high at maxima; with internal measurements somewhat so; with 1 long bristle, flanked by 2 small ones, near dorsocaudal angle. Metepisternum (MTS.) with 1 long bristle in upper rear quadrant, in line with long, narrow squamulum (SQ.), which is thrice as long as broad at middle and is inclined ventrocaudad about 20° from horizontal. Metepimere (MTM.) usually with bristles arranged 4–3–3 in ♂, 4–4–3 in ♀, excluding small intercalaries in last row, 1 of which extends above and below row, and which may be double above ventralmost long bristle; with caudal margin evenly biconvex below level of spiracular fossa, the upper lobe 1·5 times height of lower bulge. Spiracular fossa sagittate but with base broad. Ventral margin quite straight and horizontal, dorsal margin sloping from middle to apex so that both margins parallel for basal half; about 1·8 times as long as broad at maximum level.

Legs. Metacoxa (COX. 3) with lateral bristles on apical $\frac{3}{5}$ and these submarginal or nearly so; with a group of 8 thin mesal bristles in 2 rows of 4 on ventral fifth, plus a few small, adjacent but proximal, mesal submarginals. With about 9 small, thin lateral non-marginal bristles scattered over profemur (FM.1) in 2 irregular rows along long axis. Meso- and metafemora with a group of small, widely spaced dorsal submarginal bristles along apical third and 3–4 ventromarginal ones along apical fifth, of which distal 2 quite long; with 2 bristles adjacent to spiniform member of apical pair of stout bristles. Protibia and mesotibia with apical group of stout bristles paired; stout dorsomarginals paired except for fourth pair (from apex). Metatibia (fig. 19) similar but dorsomarginal notches much more pronounced and with 1 stout bristle contiguous to apical group (A.G.) of 2. Fringe of bristles on dorsal (caudal) margin of first protarsal segment extending slightly beyond middle of II. Apical caudal bristle of mesotarsus I and II reaching to middle of II and III respectively; that of metatarsus II nearly reaching middle of III.

Measurements (in micra) of tibiae and tarsal segments (petiolate base excluded) for holotype:

		Tarsal Segments				
Leg	Tibia	I	II	III	IV	V
Pro-	223	84	84	66	42	101
Meso-	336	166	105	72	46	113
Meta-	483	407	253	138	76	125

Tarsal segment V with first pair of stout lateral plantar bristles slightly displaced towards midline on protarsus (fig. 7) and mesotarsus; not on metatarsus (fig. 8). Third pair of plantars not nearly as displaced medially on metatarsus V as on protarsus. With 2 pairs of thin mesal bristles near first lateral plantars on metatarsus V and 1 such pair by second and fifth lateral plantars; with a stouter, median apical

pair; 2 such pairs subapical (of these, 1 median); pair of pre-apical plantar bristles near midline; pre-apical plantar hairs well developed.

Abdomen. Tergum 1 (fig. 9, 1 T.) shorter than preceding notum with its flange; with 3 rows of bristles, preceded by 1–3 subdorsals. Basal sternum of ♀ with a patch of about 14–16 small lateral bristles commencing near vinculum (VC.4) and extending in 2 irregular subvertical rows to near lower third of sternum. Terga 2–5 in ♂ and 2–4 in ♀ with 1 subdorsal apical spinelet per side. Unmodified terga in ♂ with first row not reaching level of spiracular fossa and with ventralmost bristle of second row just below fossa. Caudalmost 2 rows in ♀ similar (i.e., fig. 30, 6 T.); first row ¾ length of second and preceded by a rudimentary row of 2–4 small bristles. Abdominal spiracular fossae (fig. 11, 7 SPC., ♂; fig. 26, ibid., ♀) sagittate but narrow, ranging from 2·7 times as long as broad, on tergum 6, to 1·7 times, on 2 T.; at times dorsally sinuate. Typical sterna in ♂ (fig. 11, 7 S., 7 T.) with a subventral row of 3–4 bristles of which ventral 2 long and submarginal; these preceded by 6–8 small ventromarginals in 2 irregular rows. In ♀ (figs 26, 30, 6 S.), these sterna with 3–4 bristles in first row, 5–7 in second and 5–6 in last; at least 4 ventralmost in last row long, as often is ventromarginal of second row. Upper antepygidial bristle in ♂ (fig. 11, A.B.) slightly more than half length of lower; slightly shorter in ♀ (fig. 26, A.B.). 7 T. of ♀ with modified bristles, resembling A.B., as follows: upper one (U.M.B.) submarginal; not quite as dark, nor as stout nor as long as upper A.B. Dorsalmost of lower modified bristles (L.M.B.) virtually contiguous with plate of A.B. and longer than and as stout as upper A.B. and superficially appearing as an antepygidial bristle; ventral one (L.M.B.-2) similar, but ventrocaudad of L.M.B., separated by a distance equal to height of plate of A.B. Lobe above antepygidial bases (U.L. 7) shorter than antepygidial plate in ♂; subequal in ♀. Lower lobe of ♀ 7 T. (L.L. 7) about twice length of A.B. plate; fairly acutely pointed, but margin turning sharply ventrad at level of L.M.B.-2.

Modified Abdominal Segments—Male. Tergum 8 (fig. 11, 8 T.) slightly more than twice as high (along anterior margin) as long at level of base of spiracular fossa; caudal margin extending ventrad only as far as level of subanal sclerite; i.e., scarcely below spiracular fossa; anterior margin terminating at level of ventralmost bristle of 7 T.; with 2–5 small subdorsal bristles near fossa. Spiracular fossa 8 (8 SPC.) right-angled; its ventral arm more than 5 times as long (high) (including region below horizontal or oblique portion) as broad at middle; horizontal section twice as long as broad, and twice as long as middle of upright arm is broad, gradually and slightly broadening from apex (ventral) to base; ventral extension with height equivalent to somewhat less than half diameter of horizontal section. Sternum 8 (8 S. and fig. 29) very large; about 1·3 times as long (p3–t3) as broad (high) (q3–i3) at maxima; extending dorsad above ventral margin of 8 T. and, ventrally, further cephalad than line of antepygidial plate; somewhat trapezoidal, but apparent dorsal margin (h3–j3) convex; and then remainder of true dorsal margin sloping ventrocaudad at angle of 45° to dorsocaudal corner at m3; ventral margin slightly concave at caudal third (q3–s3) or half (and thereafter microdenticulate); caudal margin (m3–t3) shallowly convex or almost straight: anterior margin (p3–l3) curving dorsocaudad at about angle of 60° and then (l3–h3) mainly at 45°. Lumacaudate process (LUM. and fig.

12) arising at middle portion of ventral margin; with truly spinose area nearly twice as long (ventrally, q3–s3) as high (level of o3) at middle; apically subovate or broadly rounded; length of apical lateral seam or fold (S. LUM.) equal to $\frac{1}{4}$ of spinose area; ventral spiniforms in general the stoutest; rest of apical and subapical heavier than median and anterodorsals; the bristles usually in 7–8 rows and about 34–42 in number. 8 S. with a curving suture (SU.8) delimiting a more heavily sclerotized mesal portion; the suture arising near dorsal margin of LUM.; curving dorsocephalad and, at dorsal third, recurving towards summit of dorsal convexity of sternum so that less tanned area commences at base of LUM. and narrows gradually. Considering only bristles caudad of suture and above and behind LUM.: 8 S. with about 18–20 bristles in 4 rows of approximately 5–6–5–4 bristles, those of the last row longer than most, and these well separated between dorsalmost (m3), which is longest, subdorsal and caudomarginal, and a submarginal group of 3 at lower third and fourth; uppermost of third row at caudodorsal corner, near m3; uppermost of second row slightly more dorsal than that of third and anterior by a distance of about $\frac{1}{2}$ its length. Remaining bristles as follows: 1 on LUM. median; a close-set group of 3–4 ventromarginals at base of LUM.; 3 oblique, irregular rows, sloping ventrocaudad, of 5–5–3, which first is anteriormost; these rows preceded by about 4 subventral small bristles. Nude area on 8 S. comprising anteroventral fourth and anterodorsal fifth. Immovable process (figs 11, 14, P.) with dorsal margin fairly straight or shallowly concave near dorsal bristle; with apical bristle more than twice length of dorsal; with caudal (ventral) margin quite straight to marked sinus at boundary with manubrium (MB.). Conical process (C.P.) of P. about 5 times as long (cf. fig. 1, e–h) as broad at middle (f–g); caudal margin fairly straight. Movable finger (F.) with portion distad of P. (s–n) slightly more than twice as long (s–n) as broad at maximum breadth near apex of P. (i–q) and nearly 4 times as long as broad at middle of subapical constriction (j–k); with broadest portion (i–q) about twice breadth of narrowest (j–k). F. with anterior margin quite convex at level of C.P. but soon straightening and then becoming mildly sinuate subapically for arc at bases of sensilla-group (S.G.); posterior margin markedly convex at apex of P. (r–q) but sigmoid so that concavity of upper half equals bulge of lower, with maximum depth of trough (k) at apical fourth. Stiva (STV.) short, the distocaudal expansion (measured from k–o, which denotes a projection of caudal margin if there were no stiva, to point p) slightly less than $\frac{2}{3}$ of j–k and about $\frac{1}{3}$ length of apex of F. (l–p). F. with a sensilla-group (S.G.) stouter but subequal in length to bristles along middle of apical margin. Distal fringe (D.FR.) with lowermost of 4 bristles thinner than its mates; with bases of lower 3 bristles recessed so that they appear somewhat submarginal and, in lower 2 bristles, distance to level where transversed by caudal margin slightly exceeding diameter of bristles at that point. With a widely-spaced group of 3 fairly long, thin bristles near beginning of sinus of caudal margin; with an oblique submedian row of scattered, thin, lateral bristles starting near pair of anterior group of mesal marginals (AN.GP.) above apex of C.P., and continuing distad to level of S.G.; middle portion of these accompanied by a few smaller mesal bristles. Fulcral sclerite (F.S.) shaped like an axe-head with a broad edge; latter (dorsal) (xx–ww) more than twice breadth of apex (zz–a3). Manubrium (MB.) broad, only slightly narrowed from middle to near apex; nearly

twice as long (y to level of a/b) (from ventral margin of tergal apodeme of segment 9, T.AP. 9, to apex) as broad at anterior ventral bulge (at w); apex (y) broad and only slightly upturned; dorsal margin slightly convex; ventral margin somewhat biconvex near base, proximal bulge (w) near level of F.S. T.AP.9 2·5–3 times as long (a/c–b/d) as broad near apex (a–c); longitudinal axis apically somewhat curving towards 8 SPC.; somewhat narrowed at middle. Sternum 9 with proximal arm (P.A.9) with margins diverging from base (gg) at trough of "U." Anterior (ventral) margin (hh–aa) quite straight and oblique (dorsocephalad) to above basal third (dd), and then curving fairly dorsad (dd–aa); upper half shallowly biconcave but with dorsal (anterior) sinus (aa–cc) longer than lower (cc–dd). P.A.9 with caudal (dorsal) margin curving dorsocaudad from trough of "U" (gg) but quite flat or mildly sinuate and in essence almost paralleling dd–aa so that upper $\frac{2}{3}$ of P.A.9 (bounded by aa, bb, ff, dd) broadly rhomboidal; and with long axis of rhombus 1·6 × cc–ee, and dimensions of arc aa–bb somewhat exceeding those of dd–ff. Distance aa–cc equals cc–ee. Distal arm of sternum 9 (figs 18, 20, D.A. 9) about 6·8 times as long (ii–qq) as broad at level (uu–jj) of transverse sclerotization (T.S.), which is narrow, straight, except for slight convexity on upper (dorsal) half of anterior (proximal) margin. Subapical notch (NCH.) on anterior (dorsal) margin parallel-sided, its depth (nn–rr) subequal to its height (mm–oo). Apical lobe (AP.L.) somewhat higher (oo–qq) than long (pp to level of rr). Thickening (THK.) at base of supramedial flap (SUP.FL.) well represented along trough of notch and slightly above and below it. Subapical lobe (SUB.L.) below notch extending slightly more dorsad than AP.L. (mm higher than pp); with a small group of thin submarginal bristles below SUB.L. Subapical group of short spiniforms (S.G.SPN.) 4 to 5 in number, with distalmost the smallest and at level of base of NCH. and basalmost at level of SUB.L. Subapical patch of "sensory" microspicules (MSP.P.) extending from near upper margin of NCH. to supramedial group (SUP.G.) of 5 thin bristles. Caudomarginal submedian group (CM.G.B.) consisting of 3 stout bristles, of which bases of upper 2 frequently overlap; with 2 much smaller, thinner marginal bristles distad of these. Mid-microspiculate area (M.MSP.) elongate-ovate, equivalent to $\frac{1}{5}$ length of D.A.9 and its cavity extending into arm for about $\frac{1}{3}$ depth of latter, its apex on anterior (dorsal margin) (kk) well separated from proximalmost bristle of group below SUB.L., at point ll.

Aedeagus—Lateral Aspect. Aedeagal apodeme (fig. 10, AE.A.) with middle lamina (M.LAM. and fig. 22) more tanned than lateral laminae (L.LAM.). Middle lamina about 4 times as long (from anterior edge of crescent sclerite, figs 23, 93 (C.S.) at base of aedeagal fulcrum, AE.F. to apex) as broad at anterior margin of bay of middle lamina (B.M.L.); anterior $\frac{2}{3}$ gradually narrowing. Apex of apodeme upturned, and plates fusing to a point just below tip, which is nearly thrice as long as broad. Apodeme somewhat constricted at level of caudal portion of caverna spiculosa (CAV.SPIC.), basad of AE.F. Lateral laminae with ventral and anterior margins primarily paralleling that of M.LAM. Bay of middle lamina (B.M.L.) extending cephalad $\frac{2}{5}$ of length of apodeme (from AE.F.). Median dorsal lobe (M.D.L.) (and fig. 42) straight but oblique at angle of about 15° commencing at constriction of AE.A. to level of middle of sclerotized inner tube (S.I.T.); here becoming markedly rounded but curving ventrad only as far as line of basal portion, at origin of hood

(HD.). Aedeagal pouch with girdle (G.) well sclerotized but narrow; ventral walls (AE.P.–V.) more tanned than girdle and lateral portions (AE.P.–L.) continuing to level of base of S.I.T.; ventrocaudal region marked by a sclerotized ovate area extending to near middle of lower margin. Hood (HD.) with a deep sinus on lower half of caudal margin; sinus reaching to near apex of sclerotized inner tube (S.I.T.) and its depth somewhat less than that of resulting lobe beneath it; this ventral lobe subtruncate dorsally and evenly and strongly convex below as margin of hood continues anterodorsad as triangular deltoid flap (DEL.FL.). Margins of DEL.FL. forming angle of 45° at junction above level of AE.F. and apex somewhat extended, acute; dorsal edge of flap blending caudally with upper apex of body of crochet (B.CR.) at base of alpha-portion (ALPH.) of Ford's sclerite (F.SC.). Ventral margin of DEL.FL. an arc whose trough is in line with bottom of phylax (PHY.) and covers region of "crochet." Lateral lobes (L.L.) extending caudad from ventral margin of AE.P. as a shallow sinuate structure and then arching to blend with lateral walls of aedeagal pouch (AE.P.–L.) and with crochet-process (CR.P.) to form quasi-crochet (Q.C.), all of which are mesal to overlapping deltoid flap (DEL.FL.). Ford's sclerite (F.SC.) largest of structures in endchamber; its alpha-portion (ALPH.) basally rectangular; its anterodorsal margin fairly straight to curve of thumblike distal section (THM.), which is short, apically truncate; curved axis of thumb about twice as long as tube-like arch is broad. Securifer (SEC.) of F.SC. chelate (in appearance) apically; dorsally biconvex, i.e., base of upper arm (U.A.) commencing as ovate structure arising near thumb of ALPH., becoming concave at caudal fourth and then with free portion of U.A. extending apicad as a narrow arched rod which is almost claw-like or falcate; with proximal axis of free section nearly horizontal and essentially an extension of that of main body of upper arm, i.e., not angling dorsally. Lower arm (L.A.) of securifer sinuate dorsally and acuminate at apex as the opposite member of the "chela." Pivotal ridge (PIV.R.) relatively lightly sclerotized; rod-like to apex at summit of phylax (PHY.) and base of F.SC. With pivotal chord (PIV.CD.) fairly straight close to basal wall of ALPH. and terminating at a root-like extension from base of U.A. Sclerotized inner tube (S.I.T. and fig. 43) lacking distinctive armature; about 9 times as long as broad at straight portion of middle; very broad basally but rapidly narrowing to a constriction at level of anterior margin of PHY., where it bulges dorsally and ventrally (with curved margins); length of dilated portion shorter than diameter; tube only slightly convex to a short dorsal spur at distal fourth and then becoming somewhat upcurved to apex; with a membranous connection between the spur and apex of tube; ventral margin extending distad of apex as a short, sinuate rod-like projection; distal fourth bearing sclerotized ring-like ridges. Crescent sclerite (C.S.) shallowly convex; about 2·5 times as long as S.I.T. is broad at middle. Satellite sclerite (SAT.S.) very small, scarcely exceeding depth of C.S. Fulcral lateral lobes (FUL.L.L.) narrow; relatively lightly tanned. Central sclerite (CEN.S.) closely approximating fulcral medial lobe (FUL.M.L.). Y-sclerite (Y.S.) conspicuous as a diamond-shaped structure below fulcrum and with a narrow branch (in lateral aspect) extending distad as floor of capsule. Dorsal virga (D.V.) lightly tanned. Lateral shafts of capsule (L.S.C.) well sclerotized from level of C.S. to ventral margin of FUL.L.L., their tendons (T.L.S.) lightly tanned. Phylax

(PHY.) conspicuous; its altitude (vertical length) about twice breadth of base; proximal half only slightly narrowing; curving dorsocaudad at upper level of S.I.T. Body (basal sclerite) of crochet (B.CR.) as long as crochet process (CR.P.); length of expanded apex equivalent to half of height of B.CR., apparently constituting major or entire component of dorsal, longitudinal portion of quasi-crochet (Q.C.); this tanned element directed caudad as an arm subequal in girth to that of B.CR.; about 6 times as long as broad at middle; slightly broadened subapically; apex broadly pointed; dorsal margin almost straight and ventral margin corresponding. Spiculose lobe (SPIC.L.) (apparent homologue of median lamella) extending below Q.C. for distance equal to half breadth of latter. Vesicle (V.) fairly well developed. Penis rods (P.R.) not extending beyond up-curve of AE.A. Apodemal rod of endophallus (third aedeagal rod) (A.P.R.) fairly well tanned to apex, near that of P.R. Ventral virga (V.V.) well developed and tanned far beyond (cephalad) level of girdle (G.).

Aedeagus—Dorsal and Ventral Aspects. (fig. 24, dorsal; fig. 25, ventral). Ford's sclerite (F.SC.) basally fused along midline. Apical half (U.A.) bifid, the cleavage extending far proximad for L.A. and ALPH. Apical lobes of U.A. broadly pointed; rather spatulate; acuminate in L.A. Aedeagal pouch not completely enclosed ventrally, its thickened ventral walls (AE.P.–V.) V-shaped, with divergence terminating at base of phylax (PHY.) and origin of lateral lobes (L.L.), which distally blend with lateral margins of aedeagal pouch (AE.P.-L.). Wall of aedeagal pouch merging with sides of crochet process (CR.P.) to form quasi-crochet of lateral aspects. Phylax (PHY.) sloping towards midline from base to apex. Spiculose lobe (SPIC.L.) arising at base of phylax and extending caudad to near apex of CR.P. Deltoid flap (DEL. FL.) triangular at caudal end as well as cephalic; covering lateral thirds of dorsal surface from origin at apex of basal sclerites of crochets (B.CR.) to level of fulcrum; likewise ensheathing sides of ventral portion of endchamber as a development of hood (HD.). Ring-like transverse sclerotizations on apical portion of S.I.T. not completely encircling tube, i.e., are ridged arcs. Crescent sclerite (C.S.) narrowed caudally as it approaches midline. Satellite sclerite (SAT.S.) along dorsal midline, immediately distal to apices of crescent sclerites and directed into chamber of sclerotized inner tube (S.I.T.). Lateral shafts of capsule (L.S.C.) appearing as long, triangular structures between lateral lobes of fulcrum (FUL.L.L.) and fulcral median lobes (FUL.M.L.) and extending to near apex of C.S. Tendons of lateral shafts (T.L.S.) arising from their bases and continuing far cephalad. Y-sclerite (Y.S.) serving as floor for capsule, with one fork or fold terminating near apex of C.S.; the other broader, butterfly-shaped, and the length of FUL.L.L. Central sclerite (CEN.S.) a bell-shaped structure superimposed upon FUL.M.L. Ventral virga (V.V.) bifid at apex. Caverna spiculosa (CAV.SPIC.) elongate, subdorsal ovate sinuses, extending from near base of bay of middle lamina cephalad towards base of aedeagal pouch.

Female. (figs 26, 27, 30). Sternum 7 (7 S.) about 1·6 times as high as long at maximum diameters; anterior margin nearly vertical save for dorsal slope towards short dorsal margin; caudal margin with upper half shallowly sinuate and lower half with a large sinus whose lower margin slopes ventrocaudad at a 45° angle and upper margin is slightly biconcave (the component arcs subequal in shape and size) and

slopes dorsocaudad at 40°; upper lobe of sinus broadly rounded; lower lobe truncate and about twice as long as broad at middle. Sternum 7 with 3 rows of bristles following a group of 2–4 small ventromarginals; first irregular and with about 10 small bristles, second with about 9, slightly longer and of these, 2 ventromarginal; third with 6 long bristles of which 1 is submedian, at level of anal stylet (A.S.), 2 near middle of upper lobe of sinus and 3 at base of lower sinus, including 1 ventromarginal and 1 sub-ventromarginal; of latter 3 on ventral lobe, anteriormost much closer to ventral member of preceding pair than to dorsal one. Tergum 8 (8 T.) with caudal margin shallowly concave to level of A.S., then quite straight and oblique to a fairly narrow lobe at ventrocaudal angle; this lobe about twice as long as broad at middle. 8 T. with an irregular row of 5 short bristles immediately in front of spiracular fossa (8 SPC.) and this preceded by 1–2 similar bristles, at times by a more anterior, smaller, dorsomarginal; ventral pair of mesal marginal genitalic bristles immediately above ventrocaudal lobe twice as long as those at base of ventral anal lobe (V.A.L.); with an oblique, horizontal row of 5 bristles near ventral margin, commencing near middle of margin and terminating at level of upper base of lobe at anteroventral angle, but anterior to it; last 3 of this row the longest; with another 2 similar rows slightly dorsad to sub-ventromarginal one, but these bristles smaller, although terminal ones get progressively longer; with a fourth such row represented merely by 1–3 bristles dorsal to these. Mesal genitalic ridge of 8 T. (M.R.8) with anterior, vertical margin slightly sinuate or almost straight; with a crescentic (quarter moon) sclerotization buttressing this, commencing at midline and continuing to subdorsal region; below the crescent, an indiscrete or Y-shaped tanned area. Dorsal anal lobe (D.A.L. and fig. 16) with anterior dorsal half and ventral two-thirds nude; remainder of surface clothed with 2 or 3 rows of bristles, of which only last complete and consisting of long bristles, especially the one above, and, particularly that below, base of anal stylet (A.S.); with an additional very long bristle at dorsocaudal angle. Anal stylet broadest near base; quite straight and cylindrical thereafter, but at times slightly narrowed at apical fourth (especially ventrally); about 4 times as long as broad at middle; with a very short dorsal bristle at base of long apical bristles; at times with a tiny ventral 1 there as well. Ventral anal lobe (V.A.L.) with distal margin bearing a pair of bristles at basal angle, viz., 1 large and 1 small; a pair of long ones near basal fifth; a very long one beyond midpoint and an adjacent smaller one (at apical $\frac{2}{3}$) and, at times, a virtually contiguous small one further distad.

Spermatheca (SP. and figs 15, 27, 31) shaped like a peanut in which the caudal lobe is foreshortened[3] and broader than the other, i.e., bulga (B.) dorsally somewhat constricted at basal third; proximal portion somewhat more convex than anterior (but lacking a distinct dorsal peak) and caudal margin somewhat flattened. Bulga about twice as long (from anteroventral angle) as broad at narrowed area; ventral margin a long, shallow arc. Hilla (H.) with nearly half its length internal; slightly more than 4 times as long (total length but excluding apical papilla, PAP.) as broad at point of entry (ignoring thickenings of wall). Apical papilla well developed,

[3] It is too bad that there is no such term as "hind-shortened," for that would be more pertinent and descriptive.

longer than high. Duct of spermatheca (D.SP. and figs 27, 31) with section entering bursa copulatrix dilated (DIL.P.) as compared to remaining $\frac{3}{4}$ of length; sclerotized internal rings best developed in region anterior to dilated section. Bursa copulatrix (B.C.) with perula (P.B.C.) ovate-oblate; anterior margin straight and vertical; caudal margin somewhat convex; twice as high as broad. Sac of bursa copulatrix (SAC.) semimembranous and dilating at level of middle of perula and extending above it for distance of 1·5–2 times breadth of P.B.C. Duct of bursa copulatrix (D.B.C.) below perula biconcave, with the arch usually quite pronounced. Duplicatura vaginalis (D.VG.) marked by an oblique sclerotization and entering at undifferentiated lura of bursa copulatrix. Glandula vaginalis (G.VG.) appearing a short, oblique slit at the termination of the virtually horizontal, somewhat thickened and muscled roof of the vagina (VAG.) near genital chamber. With an accessory "gland" (fissure) immediately anterior to G.VG. Paragenital morion (PG.M.) reduced (in mounted specimens), usually represented on each side as a narrow, short, constricted horizontal "U" near P.B.C. and whose dorsal and ventral branches are virtually contiguous and whose open end is caudad, the lumen between branches at times tanned and appearing as a short rod. Occasionally dorsal loop of PG.M. visible as an indiscrete longitudinal, membranous area extending towards ventral portion of sternum 9 (9 S.). Eighth sternum (8 S.) usually with 1 or 2 dorsal short bristles, a longer dorsal subapical one and a terminal one; apically narrow, viz., portion distad of level of most proximal bristle equal to twice breadth (height) of sternum at this level; longest bristle about 4 times this breadth.

ILLUSTRATIONS

4. Head and prothorax (♂)
5. Lateral metanotal area (♂)
6. Head (♀)
7. Apical segments of protarsus
8. Segment 5 of ♂ metatarsus
9. Meso- and metathorax
10. Aedeagus
11. Modified abdominal segments (♂)
12. Lumacaudate process
13. Dorsal and ventral anal lobes (♂)
14. Processes of clasper
15. Spermatheca
16. Anal lobes and stylet (♀)
18. Clasper and sternum 9
19. Metatibia (♂)
20. Distal arm of sternum 9
22. Apical region of aedeagus (lateral aspect)
24. Apex of aedeagus (dorsal aspect)
25. Apex of aedeagus (ventral aspect)
26. Modified abdominal segments (♀)
27. Spermatheca, genitalia and anal segments
29. Sternum 8 (♂)
30. Segments 7 (♀)
31. Genitalia (♀)
42. Apex of aedeagus
43. Sclerotized inner tube
93. Apical region of aedeagus

COMMENT. It is noteworthy that although the great majority of the long series of *M. dryadosa* were from squirrels, all of the actual hosts were species that spend all or most of the time on the ground, i.e., there were no true tree-squirrels represented. Thus, out of 1421 squirrels (excluding flying-squirrels) and tupaiids examined personally by the writer or the staff of the U.S. Army Medical Research Unit (Malaya), 149 were ground-squirrels of the genera *Lariscus* (52 specimens examined), *Rhinosciurus* (23) and *Dremomys* (74), as shown in Table 2 (p. 259), which summarizes the host-relationships of 3 Malayan *Medwayella*. These rodents nest amongst the roots of trees, etc., rather than high on the branches of the tall trees characteristic of the

Malayan forest. The other hosts occasionally reported were either ground-dwelling rats like *Rattus rajah*-group or *R. muelleri* or, like *Tupaia* (237 examined), were abundant on the ground-surface, although scansorial. In contrast, although 624 truly arboreal squirrels, such as *Callosciurus nigrovittatus* (110), *C. notatus* (259), *C. caniceps* (184), *C. prevosti* (18) and *Sundasciurus hippurus* were carefully checked for fleas, no *M. dryadosa* were ever found on them even though they inhabited the same localities and habitats as the ground-squirrels, and even though they at times carried other species of fleas. Even the 348 specimens of the small species of *Sundasciurus* (*S. tenuis* and *S. lowi*) were found to be uninfested with this new species of *Medwayella*, despite the fact that these squirrels often descend to the forest floor (but nest in trees). It also is significant that *M. robinsoni*, in contrast, could be found on any of these hosts, regardless of where they nested.

The name *dryadosa* reflects the host-relationships of this new species and derives from the Greek words *drys* or *dryas* for tree (or even from *dryados*, meaning tree-inhabitant) and *osor*, or hater. The reason for the "antipathy" of *M. dryadosa* for tree-squirrels is unknown, but it seems likely that two factors are involved, viz.: (1) Conditions in the arboreal nests of these squirrels may not be suitable for the immature stages of the flea. (2) Tree-squirrels do not spend enough time on the ground to acquire significant numbers of "strays" of *M. dryadosa*. Data concerning the 4 other species of *Medwayella* known to occur in Malaya (new species, described below) lend support to this hypothesis. Thus, all of these parasitize ground-squirrels and 2 of them have virtually never been taken on truly arboreal squirrels like *Callosciurus*. It is odd that while the fleas of ground-squirrels rarely, if ever, infest tree-squirrels, a species of flea (*M. robinsoni*) relatively common on the arboreal mammals should be reported from all the ground-dwelling species, and, indeed, at times be as prevalent on these hosts as are their "characteristic" fleas. This point is discussed further below (p. 233).

Among the ground-squirrels, *Rhinosciurus laticaudatus* was the main host for *M. dryadosa*, accounting for 65% of the records even though fewer *Rhinosciurus* were examined than any other species of small mammals listed (except for *C. prevosti*). Further consideration of the host-relationships is deferred until the end of the descriptive portion dealing with *Medwayella* in this paper (p. 258).

M. dryadosa was collected in all the non-coastal forested areas surveyed in Malaya by USAMRU, by the DMZ-IMR and by the University of Malaya, provided ground-squirrels were examined in sufficient numbers. The records include areas as far north as Kelantan and Gunong Benom. Four specimens (3 from *Lariscus*) were taken on Tioman Island, off the southeast coast of Malaya, suggesting that the species probably ranges to the forests near the east coast (where inadequate collections have been made). Altitudinally, the species is known to range from the lowland dipterocarp forest of Subang (800 ft) and Gunong Benom (700 ft) to montane forest near the summit of Mt. Brinchang at 6600 ft elevation.

2. **Medwayella arcuata** sp. nov.

TYPE MATERIAL. Holotype ♂ ex *Tupaia* sp.; INDONESIA: Sumatra, Suban Ajam, Redjang, Bengkoelen (Benkoelen or Bengkulu); July, 1916; Coll. E. Jacobson

(in the mountains 20 km from Benkoelen town, approximately 3° 15′ S, 102° 25′ E, fide F. G. A. M. Smit, in litt.). No other specimen known. Holotype deposited in Rijksmuseum van Natuurlijke Historie (Leiden).

Diagnosis. Separable from all described species except *M. javana* in that dorsal margin of distal arm of sternum 9 (fig. 33) is deeply arcuate subapically and hence lacking the true notch (NCH.) of *M. dryadosa* (fig. 20) and *M. robinsoni* (fig. 21) or flattened apicodorsal margin of *M. loncha* (figs 3, e3–qq; 127) and the new species next described (fig. 68, HOM.) and their allies. Near *M. javana* but separable as follows: (1) Movable finger (fig. 34, F.) much broader throughout, viz., portion distad of apex of immovable process P. about twice as long (cf. fig. 1, r–n)[4] as F. is broad at level of apex of conical process of P. (C.P.) (i–q) instead of about 4 times as in *M. javana* (fig. 133, F.) while length (r–n) is about 4 times breadth at level of middle of subapical constriction (j–k), not 5 times. (2) Due to curve of arc of bases of bristles of distal fringe (D.FR.), distance from uppermost bristle to apex of F. equals approximately $\frac{1}{3}$ of that to most dorsal part of curve at group of sensilla (S.G.) (l), instead of being subequal. (3) Subapical dorsal sinus (fig. 33, ARC.) deeply and almost evenly arcuate, nearly thrice as long (chord between tips of SUB.L. and AP.L., e.g., mm–pp) as deep at trough, not 5 times because of shallow depth (fig. 134, ARC.), nor with apical lobe (AP.L.) extending more dorsad than subapical lobe (SUB.L.). (4) Lower arm of securifer (fig. 98, L.A.) with caudal margin slightly sinuate and subacute at ventrocaudal angle, instead of being oblique and truncate (fig. 95). (5) Tanned portion of quasi-crochet (Q.C.) tantamount to crochet-process (CR.P.), longer and narrower in new species, i.e., nearly 4 times as long as broad at middle, instead of 2·5 times.

Descriptive notes. Otherwise essentially as in *M. dryadosa*, except as follows: Distal arm of sternum 9 with bristles between those of caudomedial group (fig. 33, CM.G.B.) and subapical group of spiniforms (S.G.SPN.) quite stout. Thumb (fig. 98, THM.) of Ford's sclerite resembling *M. robinsoni* in being short and curved. Dorsal margin of upper arm of securifer (U.A.) quite sinuate, the resulting anterior lobe subequal to length and curve of claw-like extension of U.A. Base of phylax with a pronounced caudal bulge.

Illustrations

33. Distal arm of sternum 9
34. Processes of clasper
98. Apical region of aedeagus

Comment. The name of the species is based upon the characteristic shape of the upper, anterior portion of the distal arm of sternum 9 and is the Latin adjective *arcuata* meaning bowed or curved.

3. **Medwayella angustata** sp. nov.

Type material. Holotype ♂ and allotype ♀ ex "*Sciurus nigrovittatus* and *Lariscus niobe*" (= *Callosciurus nigrovittatus* and *L. insignis niobe*); INDONESIA:

[4] Compare with fig. 1 for abbreviations of reference points used in measurements.

W. Sumatra: Sipora Island; Nov. 1924; Coll. C. Boden Kloss. Paratypes: 1 ♂, ibid.; 1 ♂, 1 ♀, ibid., but ex *C. nigrovittatus* (all from N. C. Rothschild Collection at British Museum (Natural History)). Holotype, allotype and 1 ♂ paratype deposited in collection at Tring. 1 pair of paratypes in collection of R. Traub, with ultimate deposition in the U.S. National Museum.

Diagnosis. Near *M. dryadosa* regarding truncate margin of apical lobe (fig. 36, AP.L.) of distal arm of sternum 9, etc., but separable as follows: (1) Alpha-portion (fig. 45, ALPH.) not terminating in a "thumb" (cf. figs 22, 42, 93, THM.) but, instead, with tanned portion apically rod-like and with a semi-membranous truncate extension joining base of upper arm (U.A.). In *M. dryadosa*, ALPH. terminates in a subquadrate thumb-like process thrice as long (tall) as broad. (2) Securifer with base of upper arm (U.A.) less than 1·5 times length of extended snout-like or digitoid portion, instead of being more than twice its length (measured from edge of internal vertical root. (3) Distal ⅔ of extended portion of lower arm (L.A.) acuminate, fairly straight; instead of with subapical portion narrowed significantly, and this portion up-curved. (4) Phylax (PHY.) relatively broad, i.e., only about 1·6 times as long as broad at base instead of twice as long. (5) Base of PHY. with caudal margin more convex than anterior margin which is quite straight ventrally; instead of vice versa. (6) Tanned portion of quasi-crochet (Q.C.) relatively broader, i.e., length (measured from caudal margin of phylax) only about 4·4 times girth at middle instead of 5 times. (7) Anterior ventral bulge of manubrium (cf. fig. 1, w) much more pronounced than bulge (u) caudad of sinus (v) instead of both being subequal and shallow. (8) Distal arm of sternum 9 (fig. 36, D.A.9) with notch (NCH.) asymmetrical in that lower margin (mm–nn) is longer than upper one (nn–oo), instead of notch being symmetrical, the upper and lower margins subequal (fig. 20). (9) Notch comparatively shallow, its depth (measured along edge of apical lobe, AP.L.) at middle (nn–rr) hardly more than ⅓ breadth of AP.L.; in *M. dryadosa* it is more than ⅔. (10) Upper margin of AP.L. convex before truncate apex instead of being quite flat to squared apex. (11) Female sternum 7 (figs 37, 38, 41, 7 S.) with dorsal margin of subventral sinus paralleling ventral margin for at least basal half instead of diverging almost immediately (figs 26, 30, 31). (12) With a well developed vaginal "gland" caudad to glandula vaginalis (G.VG.). This is lacking in *M. dryadosa.* (13) Paragenital morion weakly tanned, represented only by two pairs of short sclerotized parallel lines; one set at apex of G.VG. and one somewhat more anterior (fig. 41); lacking the longer rod-like sclerotization near perula of *M. dryadosa* (fig. 31, PG.M.).

Also resembling *M. robinsoni* but readily distinguishable as follows: (1) Alpha-portion (fig. 45, ALPH.) not terminating in a "thumb" (cf. fig. 23, THM.) but instead with tanned portion narrowing apically, rod-like. (2) Snout of upper arm (U.A.) relatively long and narrow, fairly straight or slightly bowed, i.e., digitoid, but very gradually narrowing from base to apex; about 5 times as long as broad at middle instead of being only 2·5–3·5 times as long as broad, more rapidly narrowing from base, and distally fairly broad. (3) Tanned dorsal margin of basal ⅔ of U.A. (the non-digitoid portion) of almost uniform breadth throughout, instead of being much broader proximally than distally. (4) Distal arm of sternum 9 (fig. 36, D.A.9) with apical lobe (AP.L.) truncate nearly its entire breadth, with only upper corner rounded

instead of with upper $\frac{1}{3}$ or $\frac{1}{2}$ convex (figs 21, 47, cf. also fig. 1, pp–qq) or at least oblique (fig. 54). (5) Notch (NCH.) in D.A.9 relatively shallow; its depth measured from level of inner edge of AP.L. (nn–rr) is only $\frac{1}{3}$ breadth of AP.L., instead of exceeding $\frac{2}{3}$ of its breadth. (6) Male 8 S. with apparent dorsal margin much longer than in *M. robinsoni*, i.e., not curving appreciably ventrocaudad until well beyond apex of immovable process P. instead of curving well proximad of apex of P. (fig. 28). (7) Lumacaudate process (fig. 39) relatively broader, i.e., the portion distad of internal seam (S.LUM.) only about 67–75 % of breadth of LUM., instead of being subequal to it (fig. 28, LUM.). (8) Anterior (ventral margin) of proximal arm of 9 S. with apical sinus (aa–cc) well developed and ventral one (cc–dd) inapparent, while both are visible in *M. robinsoni* (figs 1, 47) but aa–cc is hardly larger than cc–dd. (9) Sinus in ♀ 7 S. fairly symmetrical, i.e., dorsal margin only slightly diverging from degree of curve of ventral margin (figs 37, 41) instead of clearly doing so at apical half or two-thirds (fig. 49). (10) With a relatively tall and distinct "gland" at dorsal wall of vagina caudad of glandula vaginalis (G.VG.) (although smaller in paratype than in figure 41, which is of allotype). In *M. robinsoni* there is a small, bead-like gland here. (11) Mesal genital ridge of ♀ 8 T. (figs 37, 38, 41, M.R. 8) with dorsal, horizontal tanned area convex ventrally, not sinuate (figs 32, 49) and ventral tail-like portion shorter and stouter, about 1·5 times as long as broad, not 3–5 times. (12) Lobe at ventrocaudal angle of 8 T. ovate, not acute.

Descriptive notes. Essentially like *M. dryadosa* except as indicated above, and as follows. Tergal apodeme of segment 9 with ventral margin evenly convex instead of sinuate. Tergum 7 of ♀ with caudal margin relatively flat, not curving caudad to or beyond level of apex of lobe (L.L.7) below antepygidial bristles. Ventral margin of spiracular fossa 8 of ♀ straight.

Illustrations

35. Processes of clasper
36. Distal arm of sternum 9
37. Modified abdominal segments (♀)
38. Spermatheca, genitalia and anal segments
39. Lumacaudate process
41. Genitalia (♀)
45. Apex of aedeagus

Comment. The name *angustata* is derived from the Latin term for *narrow*, and refers to the appearance of the apex of the alpha-portion and of the upper arm of the securifer.

4. **Medwayella robinsoni** (Rothschild, 1905) NEW COMBINATION

Ceratophyllus robinsoni Rothschild, 1905, Novit. zool. 12:483, fig. 6.

Pygiopsylla robinsoni, Rothschild, 1906, Ent. mon. Mag. (2) 17:221; Rothschild, 1908, Proc. zool. Soc. Lond. 50:617; Oudemans, 1909, Notes Leyden Mus. 31:195, fig. 1; Rothschild, 1919, J. Fed. Malay States Mus. 8(3):5, pl. 2, figs 4, 5; Jordan & Rothschild, 1922, Ectoparasites, 1:230, figs 223, 224.

Stivalius robinsoni, Jordan & Rothschild, 1922, Ectoparasites, 1:259, figs 223, 224; Costa Lima & Hathaway, 1946, Pulgas: 324; Traub, 1950, Proc. ent. Soc. Wash. 52(3):121; Traub, 1951, Proc. biol. Soc. Wash. 64:11, pls. 2, 4; Smit, 1958, Bull. Brit. Mus. (Nat. Hist.) Ent. 7(2):41.

Diagnosis. The features cited in the comparison of *M. dryadosa* with *M. robinsoni* serve as a diagnosis, but since *M. robinsoni* is a widespread species, ranging at least as

far as Borneo and Indonesia, and subspecies exist, salient characters at the species-level are now cited. (1) Thumb (figs 23, 44, THM.) of alpha-portion (fig. 46, ALPH.) of Ford's sclerite short and in the "cocked" position; apically flattened and with rounded corners; somewhat longer (broader) at apex than stem is tall; anterior margin convex, posterior margin concave. (2) Upper arm (U.A.) of securifer with base quite flat dorsally and slightly exceeding THM. in height; apex digitoid but broader at base and slightly arched. (3) Lower arm (L.A.) almost as high as long at base; caudal margin oblique (75°) and quite straight; with a short, narrow lobe at ventrocaudal angle. (4) Phylax (PHY.) about 1·7 times as high as broad at base and somewhat expanded subventrally. (5) Tanned portion of quasi-crochet (Q.C.) straight; at least thrice as long as broad at middle; apical margin angled subdorsally. (6) Sclerotized inner tube long and narrow; broadest near base and then slightly arched for $\frac{1}{6}$ of length; straight thereafter; with long, oblique dorsal spur. (7) Hood (HD.) with sinus fairly deep, extending to apex of S.I.T. (8) Distal arm of sternum 9 (figs 21, 53–55) with conspicuous notch (NCH.) which is subequal—lower margin (mm–rr in fig. 1, *q.v.*) longer than upper (oo–rr), and usually conspicuously so. (9) Apical lobe (AP.L.) of D.A.9 with margin (qq–oo) sinuate; upper half (qq–pp) convex; lower half (pp–oo) straight or slightly concave. (10) Subapical group of spiniforms (S.G.SPN.) about 4 in number, short and fairly evenly spaced. (11) Transverse sclerotization (fig. 48, T.S.) somewhat sinuate. (12) D.A.9 lacking a ventro-apical rod-like extension (unlike *M. loncha* and allies, figs 3, 111, EXT.9). (13) Proximal arm of sternum 9 (P.A.9 and fig. 63) with upper half (aa–dd) of anterior (ventral) margin shallowly sinuate; upper concavity (aa–cc) taller than lower (cc–dd). (14) Posterior (dorsal) margin of P.A.9 with upright part (ff–bb) quite straight. (15) Movable finger (figs 17, 47, F.) fairly broad; region (n–s) distad of immovable process P. slightly less than 4 times as long as broad (j–k) at subapical constriction and only scarcely more than twice as long (n–s) as broad at maximum dimensions (i–q) near level of apex of conical process (C.P.). (16) Stiva short and bluntly ovate; apex of F. (l–p) about 2·2 times as long as stiva (p–o/k). (17) Sternum 8 (fig. 28) with apparent dorsal margin (h3–j3) relatively flat and very short due to slope of anterior and "posterior" margins (but actually extending to ventral third—to m3), region h3–j3 only about $\frac{1}{4}$ length of ventral margin. (18) 8 S. relatively long, its ventral length (p3–t3) about 1·5 times maximum height (i3–r3). (19) Lumacaudate process (LUM.) fairly long and narrow, nearly thrice as long ventrally (q3–s3) as broad at level of o3. (20) Female sternum 7 (figs 32, 49, 7 S.) with subventral sinus with dorsal margin usually paralleling ventral margin for about $\frac{1}{3}$–$\frac{1}{2}$ length of sinus, notch therefore generally fairly symmetrical basally. (21) Lobe below 7 S. slightly broader than sinus, of same length, and subtruncate. (22) Spermatheca (figs 32, 52) with bulga (B.) about twice as long as broad in somewhat constricted middle; with a short dorsal peak (PK.) on caudal bulge; inner dorsal margin flat on apex of anterior bulge. (23) Hilla (H.) with anterior margin entering into bulga for nearly $\frac{1}{2}$ its length, of uniform diameter except for distinct apical papilla. (24) Perula of bursa copulatrix (P.B.C.) narrowly ovate but for flattened anterior margin. (25) Sclerotized sectors of paragenital morion appearing (per side) as a single long rod above glandula vaginalis (G.VG.) and a pair of short rods near top of G.VG. (26) With an

accessory gland accompanying well developed G.VG. and nearly as large; with 2 or 3 characteristic bead-like glands lining upper wall of vagina near genital chamber, viz.: 1 or 2 near G.VG. and, at times, 1 at apical fourth. (27) Mesal genitalic ridge of 8 S. (M.R.8) resembling a "T" on edge, and with lower arm quite long and narrow; darkest at and above cross-bar, which is curved and sinuate. (28) Third vinculum (fig. 50, VC.3) with dorsal surface quite even. (29) Squamulum (SQ.) parallel to long axis of body; about 3·2 times as long as broad at middle.

COMMENT. *M. robinsoni* was described from a single female specimen collected from *Callosciurus nigrovittatus* in southern Thailand at Nawng Chik, in Pattani, one of the regions formerly called a "Siamese Malay State," and at 6° 53′ N, 101° 15′ E (fide F. G. A. M. Smit, in litt.). In 1919 Rothschild described the male "*Pygiopsylla robinsoni*" on the bases of a pair from *Tupaia tana*, from Korinchi, West Sumatra, apparently overlooking the treatment and illustration of the male by Oudemans, 1909, which referred to two pairs from a nest of *Callosciurus notatus* in Batavia. Rothschild also alluded to a pair from Java, also from *C. notatus*. In 1922, Jordan & Rothschild mentioned additional Sumatran records and illustrated variations in the spermatheca. Later in 1922 these authors summed up the records, including Oudeman's, and pointed out the "♂ is easily recognized by the spinulose process which lies on each side beneath the ninth segment." This presumably was considered so diagnostic that no further description was given at the time, nor was the male ever adequately figured by these workers. This is unfortunate, since the Indonesian specimens represent different subspecies from the mainland *robinsoni*, as is shown below. It should be noted, however, that Jordan & Rothschild were not referring to the specimen herein described as *arcuata* when mentioning material from Korinchi, Sumatra, even though the slide of the unique holotype had been identified as *robinsoni* at the Rothschild Museum at Tring. The Korinchi specimens from "Benkulen, Sumatra," mentioned in 1922 were from "Padang Bovenlanden," not from the type locality of *arcuata*, although they were likewise collected by E. Jacobson in July, 1916. It seems to me that the omission of this specimen from the cited records was deliberate and that Jordan & Rothschild realized that it was not really *robinsoni*.

M. robinsoni has not been fully described or illustrated to date, although Traub (1951) figured the spermatheca and aedeagus and referred to it when diagnosing another species of *Stivalius s. lat.*

The species is somewhat variable throughout its range in the Malayan peninsula, although the differences are sufficiently minor to be considered as individual or artificial, e.g., due to the position of the spermatheca or the movable finger, etc., in the mounted specimen. There seems to be no valid evidence of subspeciation in the material extant, ranging from northern Malaya to Johore. The type specimen of *robinsoni*, unfortunately a female, is indistinguishable from material from Selangor. For these reasons, I feel that the Malayan slides represent the nominate form even though males from the "Thai Malay States" are unknown. Further, zoogeographic data also indicate that the major faunal differences between Thailand and Malaya, at least insofar as concerns rodents and fleas, occur substantially further north. Moreover, certain Malayan rat-fleas, such as *S. klossi* (Jordan & Rothschild, 1922) and

Neopsylla dispar Jordan, 1932, range much further north without apparent subspeciation (although distinct subspecies of *S. klossi* occur in the Indo-China region and in southern China).

However, there are significant differences between males from peninsular *M. robinsoni* and those on Java, Sarawak and even Tioman Island, off the east coast of Malaya, and such subspecies are described below. There is insufficient material at hand to treat Sumatran forms, although I believe that at least one subspecies occurs on that island as well. New subspecies are described after the diagnosis of the nominate form.

4a. **Medwayella robinsoni robinsoni** (Rothschild, 1905)

Diagnosis. (1) Thumb (figs 23, 44, THM.) of alpha-portion (ALPH.) with apical margin only slightly longer than height of structure. (2) Upper arm (U.A.) of securifer with free "snout" about 3·3 times as long (measured from vertical internal root) as broad at middle. (3) Lower arm (L.A.) relatively broad; about 1·2 times as long (measured from level of apex of pivotal chord, PIV.CD.) as broad at middle; dorsal margin plunging ventrocaudad at basal $\frac{1}{3}$ or $\frac{1}{2}$ at an angle of about 60°, but margin mildly sinuate and distally slight recurved, apex blunt, not acuminate. (4) Quasi-crochet (Q.C.) with tanned portion about 4 times as long as broad. (5) Distal arm of sternum 9 (figs 1, 47, D.A.9; fig. 21) with apical lobe (AP.L.) fairly deeply sinuate, its upper half (qq–pp) quite convex; lower lobe (pp–oo) somewhat sinuate. (6) Notch (NCH.) of D.A.9 asymmetrical, lower margin (mm–nn) longer than upper margin (oo–nn); axis of notch (nn–rr) sloping ventrocephalad. (7) Female sternum 7 (fig. 49) with dorsal lobe (above ventral sinus) flattened or very shallowly concave, but lacking distinct sinus. (8) Ventral lobe of 7 S. with caudal (single) bristle usually equidistant from pair immediately cephalad, or with caudal bristle at most only somewhat closer to ventral member than dorsal member. (9) Dorsal wall of vagina (fig. 32, VAG.) caudad to glandula vaginalis (G.VG.) with 1 or 2 small knot-like or bead-like glands, 1 at about proximal $\frac{1}{4}$ and second usually near midpoint; wall fairly well tanned to near apex, at genital aperture.

Illustrations

1. Clasper and sternum 9
2. Preantennal region (♂)
17. Processes of clasper
21. Distal arm of sternum 9
23. Apical region of aedeagus
28. Sternum 8 (♂)
32. Internal genitalia (♀)
44. Apex of aedeagus
46. Apical region of aedeagus
47. Clasper and sternum 9
48. Transverse suture, D.A.9
49. Sternum 7 (♀)
50. Lateral metanotal area (♂)
51. Anal segments (♀)
52. Spermatheca
59. Genitalia and anal lobes (♀)

Comment. As shown in Table 3, the nominate, mainland form of *M. robinsoni* may be found on virtually any kind of squirrel, rat or tree-shrew in its forest-habitat. The majority of the specimens are from squirrels—*Callosciurus* or *Sundasciurus*, while *Tupaia* was also commonly infested. In general, then, the bulk of the specimens came from mammals that spend much or most of their time in trees, rather than from ground-squirrels. As indicated above, *M. r. robinsoni* is broadly distributed

throughout Malaya, and we collected it in all surveyed forested areas which were not coastal, ranging from elevations as low as 100 ft up to as high as 6000 ft. The species was rare above 5000 ft and I believe that the existing records represent recent introductions of *C. caniceps* into regions cleared of forest by man, as at the top of Mt. Brinchang or along roadsides to such high elevations. Thus, we failed to collect either *C. caniceps* or *M. r. robinsoni* on Mt. Brinchang in 1948 and 1950, before a road was cut to the summit and a radio station constructed there. When we next collected there, in the period 1955 and thereafter, *C. caniceps* was fairly common in secondary forest and on the fringes. However, more data are required to clarity this point.

It is worthy of note that *M. robinsoni* was never collected in the coastal areas of Malaya nor on the islands off the west coast, i.e., Pangkor, Sembilan I. and Langkawi I.—and neither was any other species of indigenous flea. Over 50 specimens of *Callosciurus* and hundreds of rats were examined from the coastal mainland or Langkawi (no squirrels were found on Pangkor or Sembilan I.). The only squirrel collected on Langkawi was *C. caniceps*, and specimens were shot at elevations as high at 2000 ft, and no fleas were ever noted. However, at such altitudes, the samples checked were too few to warrant conclusions on the presence or absence of *Medwayella* and other fleas. These points are discussed further, below, after the description of new species, etc.

4b. **Medwayella robinsoni peregrinata** subsp. nov.

TYPE MATERIAL. Holotype ♂ (B-48232) ex *Callosciurus notatus*; EAST MALAYSIA: W. Sarawak, Pueh; 3.VI.1958; Coll. T. C. Maa. Allotype ♀ (B-49372) ex *C. notatus*; Sarawak, (3rd Division), Bruit Isle, Rajang Delta; 22.VII.1958; Coll. T. C. Maa. Paratypes as follows: 1 ♂, 1 ♀ with same data as allotype; 2 ♂ ex *C. notatus*; S.W. Sarawak, Tapuh; 9.VII.1958; Coll. T. C. Maa. Holotype, allotype in U.S. National Museum, with holotype bearing number U.S.N.M. number 71599. Paratypes in collection of B. P. Bishop Museum (Honolulu) and that of author.

DIAGNOSIS. (1) Labial palpus extending to just beyond base of pro-trochanter instead of to (or near) apex of procoxa as in other subspecies. (2) Distal arm of sternum 9 (fig. 55) with apical lobe (AP.L.) appearing at first glance to be largely truncate, but actually upper portion (fig. 1, pp–qq) convex, and only lower, longer portion (oo–pp) quite straight. In the nominate form (fig. 47, D.A.9 and fig. 21) the 2 portions are subequal and oo–pp is concave. (3) Lower arm (fig. 57, L.A.) of securifer generally somewhat acute apically, primarily due to the fact that ventral margin is straight to near apex, instead of being sinuate and upcurved subapically (figs 23, 44) so that the tip is broadly angled. (4) Tanned portion of quasi-crochet (Q.C.) about 3·5 times as long as broad at middle, not 4 times.

Similar to the nominate form in other respects, including F., and even the details of the internal female genitalia.

ILLUSTRATIONS

55. Distal arm of sternum 9
57. Apex of aedeagus
60. Spermatheca and sternum 7
61. Genitalia (♀)

COMMENT. It may be significant that there are no records of *M. robinsoni* from North Borneo, where 4 other species of *Medwayella* are known to occur, and where members of the type-host, *C. notatus*, were examined for fleas, in one locality, namely Mt. Kinabalu at 5000 ft elevation or higher. However, even where present, *M. robinsoni* is rare at such altitudes (at least in Malaya). There have been too few collections from the foot-hills and coastal areas of North Borneo to provide adequate data in regard to the possible occurrence of *M. robinsoni*. Since this species is so widely distributed in Sarawak, one would expect a similar distribution in N. Borneo, if it were present at all, but as mentioned below in the section on zoogeography, the flea fauna of North Borneo may be significantly different from that of at least southern Sarawak.

The subspecies name is derived from the Latin word *peregrinor*, meaning to travel abroad, and was selected to emphasize the distance between the mainland nominate form and the Bornean subspecies in terms of space, if not geologic time. However, it is not necessarily implied that the spread of *M. robinsoni* or of its hosts, through the eons, was from Malaya to the islands. This point is discussed in the third paper in this series and which deals with zoogeography.

4c. **Medwayella robinsoni bogora** subsp. nov.

TYPE MATERIAL. Holotype ♂, allotype ♀ (B-78347-1) ex *Callosciurus notatus*; INDONESIA: Java, Bogor; elev. 260 m; 15.VII.1965; Coll. J. M. Stusak. Paratypes as follows: 16 ♂, 17 ♀ with same data as holotype, but collected 21.VI.1965–2.II.1966. 2 ♂, 1 ♀ ex *C. nigrovittatus*; loc. cit.; 21.VI.1965. 1 ♀ ex *Petaurista elegans*; Tjibodas; 2.X.1965. 1 ♂, 4 ♀ ex *Lariscus insignis*; loc. cit.; 3.X.1965. All collected by J. M. Stusak. Holotype and allotype deposited in U.S. National Museum, with holotype bearing U.S.N.M. number 71600. Paratypes in collections of B. P. Bishop Museum (Honolulu), that of author, and other institutions listed for *M. dryadosa* above.

DIAGNOSIS. Immediately separable from the nominate form and the new subspecies herein described in that notch in distal arm of sternum 9 (fig. 54, NCH.) is nearly symmetrical, i.e., lower margin (cf. fig. 1, mm–rr) is only slightly longer than upper (oo–rr) instead of being distinctly shorter (fig. 21). Equally characteristic is the fact that axis of notch (nn–rr) parallels the long axis of the body instead of inclining ventrocephalad. Further distinguishable from *M. r. robinsoni* as follows: (1) Height of thumb (fig. 58, THM.) of alpha-portion of Ford's sclerite about twice as broad (long) apically as high and thus not nearly as tall as in nominate form (figs 23, 44), where THM. is nearly as high as long. (2) Upper arm (U.A.) of securifer with free "snout" relatively shorter and stouter, about 2·5 times as long (measured from vertical internal root) as broad at middle, instead of 3·3 times. (3) Apical lobe (AP.L.) of D.A.9 with upper portion (cf. fig. 1, pp–qq) oblique, not convex. (4) Lacking bead-like sclerotizations on dorsal wall of vagina (fig. 62, VAG.), distad of glandula vaginalis (G.VG.). (5) With only 2 bristles on ventral lobe of sternum 7 (7 S.), not 3. (6) Female often with a "supernumerary" bristle between rows II and III of head; this is unusual in mainland *M. robinsoni* (the nominate form). Very similar to the nominate form in other essential respects.

ILLUSTRATIONS

54. Distal arm of sternum 9
58. Apex of aedeagus
62. Spermatheca, genitalia and sternum 7
63. Proximal arm of sternum 9

COMMENT. The known specimens were primarily all from *Callosciurus notatus*, but it is anticipated that this subspecies also commonly occurs on *C. nigrovittatus*. The data, although inadequate, also suggest that, like the nominate form, *M. r. bogora* readily infests other squirrels, etc., in its habitat. The name *bogora* should be regarded as a coined term, although suggested by the type-locality, Bogor.

4d. **Medwayella robinsoni tiomanica** subsp. nov.

TYPE MATERIAL. Holotype ♂ (B-55344-1) ex *Callosciurus nigrovittatus*; WEST MALAYSIA: Pahang, Pulau Tioman, on Kampong Tekek-Kampong Juara Track; elev. 500 ft; 30.III.1962; Coll. Ng Cheong Kee et al. Allotype ♀ (B-55335) ex *C. notatus*; loc. cit., but Kampong Tekek; 18.III.1962. Paratypes (all collected by Ng Cheong Kee et al. in 1962, unless otherwise indicated) as follows: 2 ♂ with same data as holotype. 2 ♂, 3 ♀ ex *Sundasciurus tenuis*; loc. cit. but 20.III. 3 ♂, 3 ♀ ex *Tupaia glis*; loc. cit. but elev. 150–500 ft; 20-23.III. 2 ♂ ex *Lariscus insignis*; loc. cit. but elev. 150 ft; 22.III. 3 ♀ with same data as allotype but 18-19.III. 1 ♂, 2 ♀ ex *C. nigrovittatus*; loc. cit. 3 ♂, 1 ♀ ex *T. glis*; loc. cit. but 2.V.1966; Coll. M. Nadchatram. 1 ♀ ex *L. insignis*; loc. cit. but 1.V.1966; Coll. M. Nadchatram. 7 ♂, 3 ♀ ex *Iomys horsfieldi*; Kampong Juara; elev. 150 ft; 25-31.III. 2 ♂, 2 ♀ ex *S. tenuis*; loc. cit. but 11.IV. 10 ♂, 4 ♀ ex *T. glis*; near camp; elev. 50-1000 ft; 8-9.IV. 1 ♂ ex *Rattus t. tiomanicus*; loc. cit. but elev. 500 ft; 9.IV. 5 ♂, 4 ♀ ex *T. glis*; Ulu Sungei Ayer Besar; elev. 800-900 ft; 9-11.IV. 1 ♂ ex *L. insignis*; loc. cit. but elev. 900 ft; 10.IV. 1 ♂, 1 ♀ ex *R. sabanus*; loc cit. but 11.IV. 2 ♂, 1 ♀ ex *T. glis*; Kampong Mokut; 9.IV. 1 ♂ ex *L. insignis*; Ulu Lelang, 17.IV. 1 ♀ ex *R. surifer*; loc. cit. but 16.IV. 1 ♂ ex *C. notatus*; Pulau Tulai, 6 mi NW of Pulau Tioman; 4.IV. 1 ♂, 1 ♀ ex *C. notatus* nest; loc. cit. Holotype (U.S.N.M. No. 71601) and allotype deposited in U.S. National Museum. Paratypes in that institution, the British Museum (Natural History), B.P. Bishop Museum (Honolulu), University of Malaya and Institute for Medical Research (both Kuala Lumpur) and the author's collection.

DIAGNOSIS. (1) Apical lobe (fig. 53, AP.L.) with upper portion (cf. fig. 1, pp–qq) rather oblique and straigt instead of being convex as in the nominate form (fig. 21, 47); not nearly as vertical as in *M. r. peregrinata*. (2) Thumb (fig. 56, THM.) of alpha-portion of Ford's sclerite with stem shorter than nominate form, the untanned vertical portion definitely shorter than distal breadth, instead of only slightly so. (3) Lower arm (L.A.) of securifer with free portion proportionately longer and narrower than in mainland form e.g., length (measured from level of apex of pivotal chord, PIV.CD.) about 1·5 times as long as high at that level, not merely 1·2 times. Relative narrowness of extended part of L.A. applies to apical excised region as well as proximal section. (4) Lacking bead-like sclerotizations on dorsal wall of vagina (fig. 64, VAG.) distad to glandula vaginalis (G.VG.) which are characteristic of the

nominate form. (5) Ventral lobe of sternum 7 (7 S.) subequal to lobe above it, instead of being definitely larger.[5]

ILLUSTRATIONS

53. Distal arm of sternum 9
56. Apex of aedeagus
64. Spermatheca, genitalia and sternum 7

COMMENT. *M. r. tiomanica* infests a variety of squirrels and small mammals of similar habit and habitats in the forest on the hills of Tioman Island, primarily *Tupaia* and tree-squirrels, thereby paralleling the mainland form.

5. **Medwayella phangi** sp. nov.

TYPE MATERIAL. Holotype ♂ and allotype ♀ (B-46948-1) ex *Sundasciurus tenuis*; WEST MALAYSIA: Selangor, Subang; elev. 500 ft; 30.X.1957; Coll. R. Traub. Paratypes (48 ♂, 19 ♀) as summarized in Table 1 (p. 216). Holotype (U.S.N.M. number 71602) and allotype in collections of U.S. National Museum. Paratypes distributed as for *M. dryadosa*.

DIAGNOSIS. Male instantly separable from *M. dryadosa* and *M. robinsoni* in that dorsal margin of distal arm of ♂ sternum 9 is apically homolate (uniformly flat) (fig. 68, HOM.) terminating in an apical nubbin or short claw, instead of bearing a distinct subapical notch (fig. 20, NCH.) and an apical truncate or sinuate lobe (fig. 21, AP.L.). Further distinguishable from these species in that :(1) Quasi-crochet (fig. 71, Q.C.) is narrowed, elongate, its length, measured along entire ventral margin, more than 2·5 times length of base of phylax (PHY.) and upcurved; instead of being of quite uniform breadth, straight and short (at most only somewhat longer than base of PHY.), (figs 22, 23, Q.C.). (2) Dorsal region of Ford's sclerite characterized by a groove-like process (fig. 71, GRV.) formed by the close appression of the inner faces of the anterior portions of alpha-portion (ALPH.) and elongated base of upper arm (U.A.) of securifer, the tanned and parallel margins creating the effect of an open tube. *M. dryadosa* and *M. robinsoni* with Ford's sclerite lacking narrow groove; and instead apex of alpha-portion is thumblike (figs 22, 23, THM.). (3) Deltoid flap (DEL.FL.) very narrow due to great depth and height of sinus in hood, which extends far cephalad and hence exposing apex of phylax (PHY.) and body of crochet (B.CR.), instead of being broad and covering all of apical sclerites except tips of securifer (U.A. and L.A.) and crochet process (CR.P.). (4) Pivotal chord (PIV.CD.) well tanned and upcurved caudally instead of being lightly sclerotized and straight. (5) Movable finger (figs 65, 66, F.) with distal fringe of bristles (D.FR.) with bases of upper 4 in a straight line, and caudal margin also straight here, instead of line of bases of D.FR. and adjacent caudal margin each forming an arc (figs 14, 17). (6) Margins of F. below D.FR. fairly strongly curved and subparallel to near apex of immovable process P. (level r–s in fig. 1, *q.v.* and *cf.*) not with a slight curve to F. and margins diverging at midline so that both are rather convex at level of conical process

[5] If the specimen has been distorted in mounting, one side may appear larger than the other. Both sides should be similar in appearance before interpretations are made.

(C.P.) (i–q). (7) Male sternum 8 (fig. 69) with distinct microtufts on caudal $\frac{1}{3}$ or $\frac{1}{4}$ of ventral margin; not microdenticulate (fig. 29, s3–t3). (8) Upright portion (bb–ff) of dorsal (proximal) arm of sternum 9 mainly convex; not flat as in *M. dryadosa* (fig. 18, P.A.9). (9) Upper lobe of ♀ sternum 7 (figs 75, 76, 7 S.) slightly concave above subventral sinus, not convex (figs 26, 49). (10) Perula of bursa copulatrix (fig. 77, P.B.C.) long and mainly vertical, e.g., vermiform, its caudal margin well tanned and resembling a shallow, straight arc; sac of B.C. (SAC.) dilated and long (sausage-shaped) paralleling it; instead of P.B.C. being short and oblate-ovate and SAC. quadrate above and behind it (figs 31, 32). (11) Paragenital morion (PG.M.) well developed, several times longer and broader than glandula vaginalis (G.VG.); not merely subequal to it.

Near *M. rhaeba* (figs 138, 139) from Mt. Dulit, Sarawak, and known only from 1 pair and agreeing with it as follows: (1) With a groove-like process (fig. 71, GRV., *M. phangi*) on Ford's sclerite. (2) Upper arm (U.A.) of securifer (SEC.) relatively long and narrow. (3) Quasi-crochet (Q.C.) long, subapically narrowed and upturned. (4) Distal arm of sternum 9 (fig. 69) lacking a subapical notch; dorsal (anterior) margin rather flat (HOM.) between apex and subapical lobe (SUB.L.). (5) posterior region of ventral margin of ♂ sternum 8 microtufted (fig. 69, 8 S.). (6) Female sternum 7 (fig. 76) shallowly concave above subventral sinus.

Markedly differing from *M. rhaeba* as follows: (1) in new species, constricted portion of movable finger (fig. 66, F.) below distal fringe (D.FR.) (e.g., region marked j–k in fig. 1) almost as broad as region above it, whereas in *M. rhaeba* (fig. 138) j–k is $\frac{1}{2}$ width of apex (l–p). (2) Caudal margin of F. only somewhat convex at level of apex of P. (r), its breadth here equal to less than $\frac{1}{2}$ length of F. above P. (n–s); not so grossly convex that breadth equals more than $\frac{1}{2}$ of n–s. (3) F. so little curved that caudal margin below D.FR. is shallowly concave, instead of being so strongly arched that dorsocaudal angle (tip of stiva) (p) is in a plane with ventrocaudal tip of fulcral sclerite (F.S.) (a3). (4) The pair of longish thin bristles on caudal margin of F. well distad of the middle of sinus, closer to D.FR. than to apex of P., instead of being closer to P. than to D.FR. as in *M. rhaeba*. (5) Apical margin of distal arm of ♂ sternum 9 (fig. 68) flattened (qq–ss) and tip (qq) extending slightly as a short, straight nubbin, whereas in *M. rhaeba* the top is somewhat convex and bears a distinct tooth-like projection (qq) which is somewhat curved (fig. 138). (6) Upcurved, narrowed portion of quasi-crochet (fig. 71, Q.C.) shorter, its length (measured along ventral margin) much less than distance from base of process to ventral angle, instead of slightly exceeding it. (7) Upper arm (U.A.) of securifer slightly arched in new species, not straight. (8) Sinus near ventral margin of ♀ sternum 7 (fig. 76, 7 S.) more acute than in *M. rhaeba*, making an angle of about 23° with horizontal, not 30° (fig. 139). (9) Tergum 8 of ♀ (fig. 77, 8 T.) with a lobe at ventrocaudal angle; this apparently lacking in *M. rhaeba*.

Readily separable from *M. javana* and *M. arcuata* by the characters cited as numbers 1–4 above in comparison with *M. dryadosa* and *M. robinsoni*. Further distinguishable from *M. javana* by the following: (1) F. fairly broad subapically (fig. 66), breadth immediately below D.FR. (j–k) being almost $\frac{1}{3}$ of length from this level to apex (j/k–n) instead of being narrow, less than $\frac{1}{2}$ of length above it, as in *M. javana*

(fig. 133). (2) Quasi-crochet (fig. 71, Q.C.) more than twice as long as base of phylax (PHY.) instead of only slightly longer (fig. 95). Distingiushable from *M. loncha* at a glance, viz., (1) D.A.9 (fig. 67) lacking conspicuous spur (mm) at middle of anterior (dorsal) margin (fig. 127). (2) Quasi-crochet (fig. 71, Q.C.) long and narrow, about thrice as long as broad at base instead of being short and broad, only about twice as long as broad (fig. 128).

DESCRIPTION. Essentially as in *M. dryadosa* except as noted in diagnosis above and as follows: Mesepisternum with lobe at cephaloventral corner virtually straight.

Male. Lumacaudate process (fig. 69, LUM. and fig. 70) not as well developed—viz., lateral apical seam or flap inapparent; process shorter, apically more narrowed and not as heavily armed with spiniforms, either in number or regarding modification, i.e., with only 5–6 transverse rows of short, stout, slightly curved bristles of subspiniforms which are well separated from one another, instead of 12–16 rows of close-set modified bristles of which apical and ventral ones, especially, are true spiniforms (i.e., short, dark, basally widened, curved and broad to near pointed apex, etc., as in fig. 12); LUM. subapically only about $\frac{2}{3}$ as broad as near base instead of being subequal. Male with upper antepygidial bristle only $\frac{1}{3}$ length of lower one. Distal arm of ♂ sternum 9 with supramedial flap (fig. 69, SUP.FL.) possessing fairly short and weakly sclerotized thickening (THK.) on base, and that is apical. SUP.FL. extending to apex of D.A.9. Dorsal (upper) margin of securifer, i.e., basal $\frac{1}{2}$ of upper arm (fig. 71, U.A.) concave so that entire structure is biconcave dorsally; free portion of U.A. with basal axis somewhat upcurved (about 40° from axis of base). Lower arm (L.A.) apically truncate but lower angle rather acuminate and with tip usually recurved and hence often obscured. Ventral margin of base of S.I.T. broadly convex to level of dorsal triangular thickening (which is not spur-like) at apical third. Apex of S.I.T. with ventral margin extended caudad. Phylax (PHY.) nearly twice as high as broad at base. Quasi-crochet (Q.C.) somewhat boomerang-shaped; ventral angle rounded; proximal portion slightly exceeding distal; broadest at angle; upturned distal portion with ventral margin shallowly concave; upper margin curving at distal $\frac{1}{4}$ so that apex is ovate dorsally. (Note—Caudomarginal submedian group of bristles, CM.G.B., on D.A.9, usually with 3 stout bristles, not 2 as in specimen drawn in figure 68.)

Female. Sternum 7 (figs 76, 77, 7 S.) with ventrocaudal lobe somewhat too 'ong and broad to be an inverted, reversed image of sinus above it. Mesal genitalic ridge of 8 T. (figs 72, 77, M.R.8) consisting of a broadly crescentic sclerotization with short, broad, sinuate tail extending caudad and an indefinite tanned stalk arising from ventral base of crescent. Sternum 8 relatively broad, length distad to level of basal (most anterior) bristle subequal to breadth of segment at that level (or shorter), with about 4–6 bristles of which all but 1 of apical ones are dorsal and subapical; lower apical bristle the longest, but this shorter than twice breadth of 8 S. at level of basal bristle. Spermatheca (figs 74, 77) with dorsal constriction nearer to middle than to caudal $\frac{1}{3}$; bulga (B.) about 2·4 times as long (middle longitudinal axis) as broad at constriction; dorsal peak on caudal bulge short, inapparent unless spermatheca seen in full lateral aspect. With internal sector of hilla (H.) shorter than external portion.

Sac of bursa copulatrix (SAC.) an indefinite, long, tubular, dilated, sausage-like structure about 3–4 times as broad as diameter of B.C. near orifice to vagina. Spermathecal duct (D.SP.) with dilated portion (DIL.P.) equal to diameter of SAC. and then gradually narrowing so that at middle its diameter is ½ that of DIL.P. and anterior ⅓, about ⅛. Perula (P.B.C.) usually subvertical and quite straight except for cephalad gradual curve of extremities, or else resembling a flattened arc with concavity anterior. Glandula vaginalis (G.VG.) a straight but oblique tanned slit, about thrice height of small accessory "gland" between it and unmodified orifice of B.C. Dorsal wall of vagina well developed caudad of G.VG. and here with marginal striae or bands. Paragenital morion (PG M.) highly developed, consisting on each side of a tube-like coil surrounding all but the rear of an ovoid lightly tanned core, and occupying most of the region between P.B.C. and lower part of sternum 9 (9 S.).

Illustrations

66. Processes of clasper
68. Distal arm of sternum 9
69. Sternum 8 (♂)
70. Lumacaudate process
71. Apical region of aedeagus
72. Tergum 8 (♀)
73. Anal lobes and stylet (♀)
74. Spermatheca
76. Sternum 7 (♀)
77. Spermatheca, genitalia and anal segments

Comment. The species is named for Phang Ong Wah, who has faithfully served USAMRU (Malaya) as a collector and careful observer of small mammals and ectoparasites in Malaya, North Borneo and Sarawak since 1948, despite the arduous labor and physical danger (from both disease and hostile guerillas) that the field-work often entailed. Mr Phang was responsible for the collection of many of the specimens and new species of fleas and trombiculid mites studied by the writer, and also contributed significantly to our investigations on the chemoprophylaxis, treatment, control and ecology of scrub typhus.

A distinctive subspecies of *M. phangi* occurs in Sarawak and the nominate form will therefore be characterized before the description of the Bornean one, and before a discussion of the host-relationships and distribution of the Malayan form.

5a. **Medwayella phangi phangi**

Diagnosis. (1) Movable finger (fig. 66, F.) with distance between basal bristle of distal fringe (D.FR.) and apex of F. subequal to breadth of F. at subapical constriction. (2) Concavity of caudal margin of F. shallow; this arc with its chord about 9 times its height. (3) D.A.9 (fig. 68) with homolate margin (HOM.) relatively long in that the slope of the subapical lobe (SUB.L.) is fairly abrupt, terminating at basal ⅛ of distance between apex of SUB.L. and tip of D.A.9 (mm–qq in fig. 1). (4) Distance mm–qq scarcely exceeding that between apex of SUB.L. and distal margin of median microspiculose area (M.MSP.) (mm–kk). (5) Sinus above ventral lobe of ♀ sternum 7 (fig. 76, 7 S.) subequal to lobe beneath it. (6) Paragenital morion (fig. 77, PG.M.) with a thin transverse sclerotization across anterior portion of core.

Host-relationships and distribution and other comments. It is noteworthy that more than 90% of Malayan *M. p. phangi* (the nominate form) were from

Tupaia glis or *Sundasciurus tenuis* or *S. lowi* and that there were only 2 records from any of the truly arboreal squirrels (Table 2, p. 259), and only 1 specimen was found on a rat, even though the *Callosciurus* and *Rattus* constituted the largest categories of hosts examined. The absence of *M. p. phangi* from *Dremomys* and *Rhinosciurus* and the dearth of records from *Lariscus* is also striking.

The geographic and ecological distribution of this flea in Malaya is unusual and merits further study, but available data are summarized in Table 1 (p. 216). Although over the years since 1947, both USAMRU and DMZ-IMR collected mammals and fleas more intensively in the dipterocarp forest in the foothills around Kuala Lumpur (i.e., the forest reserves at Gombak, Ampang, Ulu Langat and Bukit Lagong areas) than in any other region or habitat, only 4 specimens of *M. p. phangi* were ever found there. In contrast, 27% of the specimens (and 30% of the numbers of collections, i.e., the hosts infested with *M. p. phangi*) were made from the secondary forests of Subang, which is also in Selangor and equidistant from Kuala Lumpur with the other areas, but at slightly lower elevation (viz., 400–700 ft versus 1000–2000 ft). Further, 40% of the specimens (35% of the collections) were from the foothills of Perak, 8–10 miles from Ipoh at elevations of about 1100 ft. This would at first glance suggest that the distribution might be an altitudinal one, a possibility that is reinforced by the absence of records from montane hosts like *Dremomys* and *Tamiops mcclellandi*. However, *M. p. phangi* is not really a lowland species, because 15% of the specimens came from Kedah Peak, at elevations often above 3000 ft, an area where relatively little collecting of ectoparasites was done by our teams and colleagues.

One likely explanation is that *M. p. phangi* is essentially a flea of secondary or disturbed forest, rather than primary forest, for all of the sites where it has been taken in reasonable numbers are regions where there has been much cutting of timber over the years or where there is an abundance of limestone formation and a dearth of the huge dipterocarps associated with primary forest in Malaya. The forest reserves of Selangor, on the other hand, have been much less altered by man, and the areas surveyed were not in limestone terrain. Another factor worth checking is that of rainfall, for the Perak and Kedah Peak collections happened to have been made during periods of relative drought. The one-to three-week dry-spells noted annually or semi-annually in most of the southern two-thirds of Malaya do not occur at fixed periods of the year, and no special effort was made to collect *Tupaia* and *S. tenuis* in the dipterocarp forest during those irregular periods. Hence data are lacking whereby this point could be determined regarding the forested belts in Selangor.

However, the distribution of *M. p. phangi* may prove to be due to zoogeographic factors, for like another new species described below and known only from west-central Malaya, it occurs in Sarawak as a distinct subspecies. Definite faunal relationships may exist between these two regions, as mentioned anon, and as discussed in the third paper in this series.

Further discussion on the host-relationships of *M. p. phangi* will be found in the comments following the descriptive sections on *Medwayella*.

M. p. phangi also occurs in extreme southern Thailand (Nakhon Si Thammarat), where a single female was collected on an unidentified squirrel by Dr Boonsong

Lekagul and kindly sent to us by Dr R. E. Elbel. It seems significant that no additional specimens of *M. phangi* turned up in the rather extensive collections of fleas made in Thailand by Dr Elbel, for the vast majority of Elbel's Thai specimens were taken north of the Malayan peninsula. In these "non-Malayan" provinces of Thailand, a new species of *Medwayella*, described later in this paper, was commonly found on *Menetes berdmorei*, a ground-squirrel and it is of interest that this new species was also taken at Nakhon Si Thammarat.

5.b **Medwayella phangi tana** subsp. nov.

TYPE MATERIAL. Holotype ♂ (B-48275-1) and allotype ♀ (B-48275-3) ex *Tupaia tana*; EAST MALAYSIA: W. Sarawak, Pueh; 11.VI.1958; Coll. T. C. Maa. Paratypes as follows: 5 ♂, 5 ♀ with same data as holotype. 1 ♂ ex *Callosciurus*; loc. cit. 5 ♂, 6 ♀ ex *T. tana*; Sarawak, Kuching, 5th mile, Stapok Rd.; IX.1951; Coll. T. Harrison. Holotype (USNM number 71603) and allotype in collection of U.S. National Museum. Paratypes in B. P. Bishop Museum (Honolulu), the British Museum (Natural History) and the author's collection.

DIAGNOSIS. Close to nominate form, and differentiated as follows: (1) Movable finger (fig. 65, F.) narrower and more arched below distal fringe (D.FR.), viz., fringe set on a low "stalk" in the Sarawak form—breadth of F. at constriction (indicated as j–k in fig. 1) much shorter than distance between basal bristle of fringe and apex of F. instead of being subequal; the arc formed by caudal margin of F., e.g., between D.FR. and where margin crosses apex of immovable process P. (k–r) quite deep, e.g., with chord equal to 4·5 times of altitude, instead of about 9-fold. (2) Apex of D.A.9 (fig. 67) with homolate margin (HOM.) comparatively short because slope of subapical lobe (SUB.L.) commences at basal $\frac{1}{3}$ of distance between tip of SUB.L. and apex of D.A.9 (mm–qq), instead of basal $\frac{1}{5}$ (fig. 68). Distance mm–qq nearly twice that between apex of SUB.L. and distal margin of median microspiculose area (M.MSP.) (mm–kk) instead of scarcely exceeding it. (4) Sinus above ventral lobe of ♀ sternum 7 (fig. 75, 7 S.) definitely shorter and narrower than lobe below it, instead of being subequal (fig. 76, 7 S.). Paragenital morion with a tanned chord along ventral margin of inner core, near its apex. In nominate form there is instead a thin transverse sclerotization curving towards middle of or dorsal part of core (fig. 77, PG.M.).

ILLUSTRATIONS

65. Processes of clasper
67. Distal arm of sternum 9
75. Sternum 7 (♀)

COMMENT. The name of the subspecies denotes a common host, *Tupaia tana*, as per existing records. However, collections in Sarawak have been too limited in general to determine whether the Bornean subspecies regularly infests ground-squirrels or other hosts.

6. **Medwayella limi** sp. nov.

TYPE MATERIAL. Holotype ♂ (B-45230) ex *Rhinosciurus laticaudatus*; WEST MALAYSIA: Selangor, Kepong, Bukit Lagong; 25.VII.1956; Coll. R. Traub.

Allotype ♀ (B-52520) ex *R. laticaudatus*; Selangor, Ampang Reservoir; 13.I.1960; Coll. J. R. Audy. Paratypes as follows: 4 ♂ with same data as holotype. 2 ♂ ibid., but 31.X.1956. 1 ♂ with same data as allotype. 2 ♂ ibid., but 16.VIII.1960; Coll. J. R. Audy. 10 ♂, 2 ♀ Selangor, Ulu Langat Forest Reserve; 21.I–18.II.1965; Coll. Lim Boo Liat. 1 ♂ ibid., but 15.I.1957; Coll. R. Traub. 3 ♂, 1 ♀ Selangor, Ulu Gombak Forest Reserve, 16–17 mi N of Kuala Lumpur; 22.VIII, 4.X, 16.XII.1956; (R.T.). 1 ♂ ibid., but 30.IX.1968; (L.B.L.). 2 ♂ Selangor, Pahang Road, 16 mi N of Kuala Lumpur; 5.VII.1948, 7.III 1956; (R.T.). 4 ♂, 1 ♀ Trengganu, Sungei Tong Forest Reserve; 26.VIII.1965; (L.B.L.). 2 ♂ ex *Lariscus insignis*; Selangor, Ulu Gombak, 15–16 mi N of Kuala Lumpur; 1500 ft elev.; 22.VII.1957, 11.VI.1958; (R.T.). 1 ♂ Trengganu, Bukit Besi; 5.VIII.1958; (R.T.). 1 ♂ ex *Tupaia glis*; loc cit. 1 ♀ ex *Rattus sabanus*; Selangor, Ampang Reservoir; 28.VII.1960; (R.T.).

Holotype (U.S.N.M. number 71604) and allotype deposited in U.S. National Museum. Paratypes distributed as for *M. dryadosa.*

Diagnosis. Very close to *M. phangi* but distinguishable as follows: (1) Groove-like process of Ford's sclerite (fig. 82, GRV.) incomplete apically due to fact that thickened ventral margin of base of upper arm (U.A.) does not extend as far dorsally as does the opposite member of the furrow, and instead terminates well before apex. In *phangi* (fig. 71) the edges of the groove parallel each other all the way to apex. (2) Apex of anterior member of GRV. extending over and beyond (dorsad) base of U.A. as a broad, truncate and squared flap whose caudal margin parallels its anterior one, and which crosses base of U.A. at anterior ¼. In *phangi*, this flap does not reach dorsal margin of base of U.A. and its caudal margin is convex. (3) Free extension of U.A. (snout) more upright, making an angle of about 45° with longitudinal axis of base of U.A. instead of only about 20–25°. (4) Free portion of lower arm (L.A.) quite narrow subapically due to slope of 60° of upper (dorsal) margin and emargination of ventral one. In *M. phangi*, upper margin sloping at 80° and ventral margin straight to near apex. (5) Tongue-like apical portion of quasi-crochet (Q.C.) shorter, due to Q.C. being angled at apical ⅓ instead of near midpoint (fig. 71). (6) Phylax (PHY.) with base much broader; its height only less than 1·4 times length of ventral margin instead of nearly twice as high. (7) Subapical lobe (fig. 81, SUB.L.) of D.A.9 with its height equal to twice that of nubbin at apex (indicated as qq in fig. 1) and with homolate margin (HOM.) correspondingly shortened, e.g., flat surface between qq and mm shorter than breadth of D.A.9 at level of apex of M.MSP. (kk) instead of with SUB.L. about subequal to apical nubbin (figs 67, 68) and HOM. longer than D.A.9 is broad at level of kk. (8) Movable finger (fig. 80, F.) with bases of distal fringe of stout bristles (D.FR.) making an oblique line with longitudinal axis of F. (n–s), not a subparallel one (fig. 66). (9) Mesal genital ridge of ♀ 8 T. (fig. 79, M.R.8) with ventral arm longer, thinner and more discrete than in *M. phangi* (fig. 77), e.g., ventral tanned area clearly exceeding in length the more dorsal oblique sclerotization; and that of the median ovate ventral bulge. (10) Perula of bursa copulatrix (P.B.C.) with sclerotized caudal margin essentially straight or slightly concave (e.g., with sinus caudal) instead of being arched (convex dorsally) or with at least upper and lower fourths curving cephalad. (11) Paragenital morion (PG.M.) with a subventral sclerotization rather than a transverse one approaching dorsal margin. (12) Ventral

lobe of sternum 7 (7 S.) taller than long, instead of with subequal dimensions. (13) Glandula vaginalis (G.VG.) 4 or more times length (height) of accessory "gland" (cleft) preceding it, not merely thrice as long.

In other respects *M. limi* is essentially like *M. phangi*. The diagnostic features cited under *M. phangi* serve to separate *M. limi* from *M. dryadosa*, *M. robinsoni*, *M. arcuata*, *M. loncha*, etc.

ILLUSTRATIONS

78. Spermatheca (variation in aspect)
79. Spermatheca and genitalia
80. Processes of clasper
81. Distal arm of sternum 9
82. Apex of aedeagus
83. Lumacaudate process
84. Spermatheca and genitalia
85. Sterna 8 and 9 (♀)

COMMENT. The species is named in honour of Mr Lim Boo Liat of the Division of Virus Research and Medical Zoology of the Institute for Medical Research, Kuala Lumpur, as partial acknowledgement of the tremendous assistance he has rendered the author and other members of USAMRU in their research on vectors and reservoirs of infection in Malaya and Borneo. Ever since 1948, Mr Lim not only collected mammals and ectoparasites with us or for us, but provided identification of hosts and served as major-domo, interpreter or liaison officer on innumerable field-trips and often under very difficult circumstances. Mr Lim also participated in Lord Medway's expedition to Gunong Benom, and, also, in his own right has contributed a great deal to the knowledge of the role of ectoparasites and small mammals in infections in Southeast Asia and in popularizing the study of natural history in that part of the world.

M. limi is a sibling species of *M. phangi* and it is of interest that the two species appear to differ significantly regarding host and habitat. Virtually all the records of *M. limi* are from the ground-squirrel *Rhinosciurus laticaudatus*, while the great majority of its sister-species were collected from *Sundasciurus tenuis* and *Tupaia*, and it was never found on *Rhinosciurus*. While nearly all of the *M. limi* were taken in the dipterocarp forests in the foothills near Kuala Lumpur, it probably is distributed in similar habitats throughout Malaya, since it was also collected in such terrain in Trengganu. There are no records from the lowland forest at Subang nor from the limestone hills of Ipoh, which were the main source of *M. phangi*. Both host-wise and with respect to micro-environment, *M. limi* resembles *M. dryadosa*, a point that is further discussed after the taxonomic portions of this article (p. 258 et seq.).

7. ***Medwayella thurmani*** sp. nov.

TYPE MATERIAL. Holotype ♂, allotype ♀ (B-15288) ex *Menetes berdmorei*; THAILAND: Nakhon Ratchasima, Si Khiu, Pak Chong; 23.IX.1952; Coll. R. E. Elbel. Paratypes, all from Thailand, as follows:

♂	♀	Host	Changwat & Locality	Date	Collector
15	8	*Menetes berdmorei*	Nakhon Ratchasima, Si Khiu, Pak Chong	IX.1952 & IX.1953	R. E. Elbel
1	–	*Rattus rajah* group	Nakhon Ratchasima, Si Khiu, Chan Thuk, Pongekeng	15.II.1953	R. E. Elbel
1	1	*Rattus rattus*	Nakhon Ratchasima, Pak Thong Chai	20.I.1967	J. F. Reinert
5	3	*Menetes berdmorei*	Nan, Pang Nam Un	19–21.I.1953	R. E. Elbel & H. G. Deignan
1	1	*Menetes berdmorei*	Nan, Sar Dist., 14 km S of Sarat Pahang	9.XII.1961	Phang Ong Wah
–	5	*Tupaia glis*	Nan, Ban Pha Hang	15–19.III.1961	K. Thonglongya
–	1	*Tupaia glis*	Loei, Dan Sai, Kok Sathon, Phu Lom Lo Mt., 2100 m	23.III.1954	R. E. Elbel & Boonsong Lekagul
3	1	*Menetes berdmorei*	Loei, same as above	29.III–2.IV. 1954	R. E. Elbel & Boonsong Lekagul
2	–	*Menetes berdmorei*	Loei, same as above	15.II.1955	R. E. Elbel
1	–	*Callosciurus finlaysoni*	Loei, same as above	17.II.1955	R. E. Elbel
3	5	*Menetes berdmorei*	Loei, Dan Sai, Na Haeo, Ban Na Muang, approx. 1780 m	9–27.X.1954	R. E. Elbel
5	2	*Tupaia*	Khon Khaen, 112–138 km on Khon Khaen–Loei Rd., 3–6 mi S of Loei Border	26.XI.–2.XII. 1962	R. Traub & J. E. Scanlon
–	1	*Menetes berdmorei*	Khon Khaen, 119 km on Khon Khaen–Loei Rd., 3 mi S of Loei Border	28.XI.1962	R. Traub & J. E. Scanlon
2	–	*Menetes berdmorei*	Chanthaburi, Klong Ta Kong, A Pong Nan Ron	22.II.1963	J. E. Scanlon
1	–	*Tupaia glis*	Chanthaburi, same as above	22.II.1963	J. E. Scanlon
–	7	*Rattus rattus*	Chanthaburi, Wad Bom Phu, A Tha Mai	21.II.1963	J. E. Scanlon
1	–	*Menetes berdmorei*	Chanthaburi, Khlung, Tapon, Khao Sabap Mt.	26.XII.1953	Boonsong Lekagul
1	–	*Tupaia glis*	Chiengmai, B. Nong Prue	15.XI.1965	D. Gould
2	–	*Menetes berdmorei*	Kanchanaburi, Trakhanum Hinlaem	9–25.XI.1952	R. E. Elbel & H. G. Deignan
–	1	*Menetes berdmorei*	Chon Buri, Si Racha, Khroa Wing	10.VII.1953	Boonsong Lekagul
–	1	*Menetes berdmorei*	Sara Buri, Kaeng Khoi, Mnak Lek, Dan Kak Sat	8.IX.1953	R. E. Elbel
–	1	*Callosciurus notatus miniatus*	Nakhon Si Thammarat, Chawang, Chang Klang, Ban Na	28.II.1954	Boonsong Lekagul
2	4	*Tupaia glis*	Khao Yai National Park, Khorat	17–24.IX.1963	J. E. Scanlon

Holotype (U.S.N.M. number 71605) and allotype deposited in U.S. National Museum. Paratypes distributed as for *M. dryadosa*.

DIAGNOSIS. Distinctive in that apical portion of dorsal margin of distal arm of ♂ sternum 9 (fig. 91) lacks a distinct notch (fig. 47, NCH.) or a long and deep arc (fig. 33, ARC.) and yet is not evenly homolate (fig. 67, HOM.) from above subapical lobe (SUB.L.) to apex. Instead it bears a small, shallow arc (fig. 91, ARC.) proximally and a scarcely differentiated, longer apical lobe (AP.L.). Also separable from known species in the hyperdevelopment of sclerotized thickening (THK.) at base of supramedial flap (SUP.FL.) of D.A.9, which here extends from ventral region of ARC. to near apex of arm. Near *M. dryadosa*, and like it in possessing a truncate thumb (figs 90, 94, THM.), as well as an acuminate extension of the lower arm (L.A.) on Ford's sclerite (cf. fig. 22, *M. dryadosa*).

Further distinguishable from *M. dryadosa* as follows: (1) Subapical lobe (fig. 91, SUB.L.) not really lobate, its proximal (anterior) margin sloping gradually to midmicrospiculate area (M.MSP.) instead of markedly angling to form a distinct projection (fig. 20). (2) Transverse sclerotization (T.S.) of D.A.9 slightly arched proximad (concavely facing base of arm) instead of being sinuate, and with concave margin facing distally. (3) Ford's sclerite with dorsal margin of base of upper arm (figs 94, 97, U.A.) quite flat instead of convex (fig. 22). (4) Lower arm (L.A.) with a dorsal spur or tooth-like projection, instead of being rounded. (5) Fusion of lateral walls of aedeagal pouch (AE.P.-L.) with crochet process (CR.P.) well tanned, resulting quasi-crochet (Q.C.) well sclerotized throughout; the darker, crochet-like structure of Q.C. less than thrice as long (measured along dorsal margin, from caudal margin of phylax) as broad at middle in *M. thurmani*. In *M. dryadosa*, comparable tanned area of Q.C. much narrower, viz., 4 times as long as broad. (6) Caudal sinus of deltoid flap (DEL.FL.) much larger, e.g., almost equal in area to apex of hood (HD.) and median dorsal lobe (M.D.L.) above it, instead of being less than ½ that size. (7) Caudal (subvertical) margin of ♂ sternum 8 (fig. 101, m3–t3) shorter; height to level of longer bristle at dorsocaudal angle (m3) subequal to length of bristle, not 25% greater than length of bristle (fig. 29), due to greater slope of dorsocaudal margin in *M. thurmani*. (8) Lumacaudate process (LUM.) narrowing from middle to apex, instead of being broadly subovate (fig. 12). (9) Female tergum 7 (fig. 99, 7 T.) with lobe below antepygidial base (L.L.7) with angle rounded off; not acute (fig. 26). (10) Anal stylet (fig. 89, S.A.) with a subapical ventral bristle. This missing in *M. dryadosa* (fig. 16). (11) Ventral lobe of caudal margin of ♀ 7 S. (figs 99, 102) almost as high as long, instead of apex about ½ as high as long (fig. 27). (12) Subventral sinus of ♀ 7 S. with basal ⅓ symmetrical, evenly curved instead of with dorsal margin sloping dorsocaudad almost immediately.

DESCRIPTIVE NOTES. Essentially otherwise like *M. dryadosa* (cf., fig. 86, head ♂ with fig. 4) except as follows. Dorsal margin of immovable process (fig. 92, P.) sinuate, but mainly convex. Mesal genitalic ridge of ♀ tergum 8 (fig. 102, M.R.8) resembling an inverted "Y" with rounded arms and a wide cleft. Spermatheca (figs 88, 102) with internal margin of bulga (B.) at base of hilla (H.) less oblique, about 35°–40°. Perula of bursa copulatrix (P.B.C.) elongate-ovoid, nearly as long as broad in middle, more dilated ventrally than dorsally; anterior margin straight and subvertical; caudal margin somewhat convex. Sac (SAC.) of B.C. small, its volume scarcely exceeding that of P.B.C., the portion immediately dorsal to perula with

height only equal to ½ that of perula. Glandula vaginalis (G.VG.) feebly sclerotized; at times inapparent; sinuate. Paragenital morion (PG.M.) weakly tanned; indiscrete, presented as a narrow, ovoid structure lying across or near base of P.B.C. and perpendicular to it.

ILLUSTRATIONS

86. Head and prothorax (♂)
87. Movable finger
88. Spermatheca
89. Sensilium and anal segments (♀)
90. Apical region of aedeagus
91. Distal arm of sternum 9
92. Processes of clasper
94. Apex of aedeagus
97. Apical region of aedeagus
99. Sternum 7 (♀)
100. Lateral metanotal area (♂)
101. Sternum 8 (♂)
102. Spermatheca and genitalia

COMMENTS. The species is named for the late Deed C. Thurman in token acknoledgement of the many and significant contributions on the ecology, control and taxonomy of arthropod-vectors of disease in Thailand which Dr Thurman managed to make before his tragic death from cerebral malaria in that country at the height of his career.

M. thurmani is predominantly a flea of the ground-squirrel *Menetes berdmorei*, with occasional specimens occurring on *Tupaia*, as can be seen from the tabulation on page 245, which summarizes the data for paratypes. *M. thurmani* is evidently a widespread species in Thailand ranging, with its main host, over most of that country, and hence I suspect that it will be found on that ground-squirrel in northern Malaya and Indo-China.

8. **Medwayella calcarata** sp. nov.

TYPE MATERIAL. Holotype ♂ (B-49517) ex *Lariscus insignis*; WEST MALAYSIA: Perak, 8 mi W of Ipoh, Kledan Saiong Forest Reserve; elev. 1300 ft; 1.X.1958; Coll. R. Traub. Allotype ♀ (B-48637) ex *L. insignis*; Perak, Maxwell Hill; elev. 3000 ft; 25.VI.1958; Coll. R. Traub. Paratypes as follows: 3 ♂ with same data as holotype; 2 ♂ ibid. but elev. 1100 ft. 2 ♂ 10 mi NW of Ipoh; 29–30.VIII.1958; Coll. R. Traub. 1 ♂, 1 ♀ Perak, Maxwell Hill, Gunong Hijau; elev. 4200 ft; 21.III.1958; Coll. R. Traub.

Holotype (U.S.N.M. number 71606), allotype and 1 paratype deposited in U.S. National Museum. Paratype (1 ♂) in the British Museum and remainder in the author's collection.

DIAGNOSIS. Separable from all described species by virtue of the modified features of the head (fig. 104, ♂), viz.: (1) Labial palpus extending to apex of protrochanter instead of only to near tip of procoxa. (2) Distal segment of maxillary palpus also unusually long—1·75 times that of segment 3 instead of about 1·5 times. (3) With additional "supernumerary" bristles (SY.) on the preantennal region, e.g., 3 instead of 1 between rows II and III, with an extra 1 in row II, in ♂ making a total of 19 long or medium-sized bristles instead of the usual 16–17. Female with 1 "supernumerary," which is absent in most ♀ members of the genus.

Agrees with *M. loncha* (figs 118, 126–132) (and the 2 new species next described) in the following respects (and thereby differing from *M. dryadosa* and allies): (1) Re distal arm of ♂ sternum 9 (fig. 111): (a) Subapical lobe (SUB.L.) long and sharp-pointed, like a spur, instead of being lobate (figs. 20, 68). (b) Apical ½ of ventral (caudal) margin (qq–u3 in fig. 3; cf., also fig. 1) much more heavily sclerotized than anterior margin e3–qq). (c) Apex of ventral margin (g3–qq) appearing to project distad of arm as a rod-like extension (EXT.9) instead of curving to form an apical lobe (figs 20, 21, AP.L.). (d) With a caudal row of about 6 wide-set, fairly long, straight spiniforms instead of a subapical group (S.G.SPN.) of close-set, fairly small ones. (e) Tanned portion of dorsal margin distad of SUB.L. (c3–f3) extending only midway to apex, e.g., to distal end of supramedial flap (SUP.FL.) and then becoming semimembranous and curving toward ventral margin, thereby accounting for the apical rod-like extension. (2) Ford's sclerite of the grooved type (fig. 113, GRV.).

Readily separable from *M. loncha* as follows: (1) Movable finger (fig. 108, F.) not nearly as short and broad, viz., length distad from apex of immovable process (P.) (cf., fig. 1, n–s) 4 times breadth of F. at narrowest level (j–k), instead of scarcely more than thrice as long as broad there (fig. 126 ,F.). (2) Bases of setae of D.FR. forming a line tangential to main axis of F. (n–s) but almost subparallel to longitudinal axis of body of flea, instead of vice versa. (3) Sinus on apical (dorsal) margin of immovable process of clasper (P.) close to caudal margin and hence resulting in a dorsocaudal lobe, instead of bearing the sinus near the anterior margin and lacking a dorsocaudal lobe. (4) Manubrium with ventral margin lacking a distinct bulge (w) immediately anterior to sinus near posterior ⅓ (v) instead of being definitely convex there. (5) Distal arm of sternum 9 (fig. 111) relatively narrow at level of subapical lobe (SUB.L.) so that breadth (cf. fig. 3) (g3–d3) is only 1·3 times length of spur (d3–mm) instead of more than twice d3–mm (fig. 127). (6) Axis of EXT.9 (g3–qq) upcurved, directed more dorsad than caudad, instead of being straight, paralleling axis of D.A.9. (7) Tanned portion of quasi-crochet (fig. 113, Q.C.) about 1·7 times as long as broad, with dorsal margin slightly concave and nearly paralleling ventral one; anterior and posterior margins slightly convex. In contrast, in *M. loncha* (fig. 128) Q.C. only 1·3 times as long as broad; dorsal margin broadly convex; ventral margin angled at middle, with anterior ½ straight, horizontal, and posterior ½ concave, curving dorsocaudad; anterior and posterior margins straight, vertical. (8) Ford's sclerite with groove (GRV.) broad and with margins equidistant and essentially parallel throughout; not narrowed at area of contact with dorsal expanded apex of body of crochet (B.CR.) and again at dorsal apex of groove. (9) Upper arm (U.A.) of securifer lacking a sclerotized nubbin at apical (caudal) ⅓ where side of lower arm (L.A.) moves dorsad to link with U.A. (10) Distance between dorsocaudal angle of apex of B.CR. and nearby dorsocaudal angle of U.A. subequal to height of slightly concave or straight apical (caudal) margin of U.A. instead of being nearly double the height of arcuate apical margin of U.A. (11) Phylax much broader, viz., only slightly more than twice as long as broad at maximum girth (near ventral margin) instead of more than thrice. (12) Dorsal spur at apical ⅓ of sclerotized inner tube (S.I.T.) curved back over tube so that for most of its length it parallels S.I.T. and is close to it instead of being oblique to it. (13) S.I.T. broad proximad of dorsal spur

but much narrowed distad (and ½ its diameter) instead of only being somewhat narrowed. (14) Angled base of subventral sinus on ♀ sternum 7 (fig. 103, 7 S.) quite diagnostic; in the other known female *Medwayella* from Malaya and Borneo the margin of the sinus is rounded (fig. 102). (15) Inner walls of sclerotized duct of bursa copulatrix (fig. 103, D.B.C.) in their entirety more tanned than bulk of perula, including anterior margin. In *M. loncha* only part of D.B.C. (fig. 118) well tanned, as is, at best, lower rear part of perula. (16) Dorsal anal lobe (fig. 103, D.A.L.) with 9 non-marginal bristles in 3 vertical rows preceding anal stylet, not with but 6 non-marginals in 2 irregular vertical rows (fig. 129). (17) Anterior margin of hilla (H.) of spermatheca protruding into bulga (B.) (internal margins) for ½ length of hilla, instead of ⅓ (fig. 132). (18) Anal stylet (A.S.) about 5·5 times as long as broad at middle, and there somewhat constricted, instead of 4·6 times and gradually narrowing from base towards apex and very slightly constricted subapically (fig. 129).

Descriptive notes. The diagnosis above serves to cite differences from *M. dryadosa* as well (q.v.) but *M. calcarata* is otherwise quite similar, except as follows.

Male. About 19 large or medium preantennal bristles in 5 irregular rows (fig. 104). Squamulum horizontal. Sternum 8 with caudal margin straight except for rounded corners; almost entire (scarcely microdenticulate) near ventrocaudal corner; long bristle near dorsocaudal angle with 2 or 3 marginal or submarginal, medium bristles above it. Lumacaudate process (fig. 107, LUM.) with dorsal margin virtually horizontal and straight; ventral margin of lobate portion oblique and usually triconvex (trebly convex); apex broadly rounded; as measured from base of ventral margin, only about 1·1 times as long as broad at base, 1·6 times as long as broad at middle bulge and 2·5 times that of subapical bulge. Movable finger (fig. 108, F.) with caudal margin quite straight at level of apex of conical process (C.P.) (cf., fig. 1, q), which in turn is only about 4·5 times as long (e–h) as broad at middle (f–g). Distal arm of sternum 9 (fig. 111) about 8 times as long (ii–qq) as broad at level (jj) of transverse sclerotization (T.S.). Distance between bulge (cc) at upper ⅓ of anterior margin of proximal arm of sternum 9 and apex of arm (aa) subequal to that from bulge (cc) to height of convexity of posterior margin (ee). Sclerotized inner tube (fig. 113, S.I.T.) with ventral margin bearing only a very short and low bulge, hence most of margin straight and paralleling dorsal one to level of dorsal spur.

Female. Caudalmost large bristle on ventral lobe of sternum 7 (fig. 103, 7 S.) approximately equidistant from dorsal and ventral members of pair preceding it. Lobe at ventrocaudal angle of 8 T. relatively long and acute; about 2·3 times as long as broad at middle. Glandula vaginalis (G.VG.) long and narrow, single (not preceded by a companion-"gland"). Mesal genital ridge of tergum 8 (M.R.8) with anterior margin sinuate at point of branch of subhorizontal arm; portion beneath fork convex, so is that of upper members of fork. Anal stylet (A.S.) long and narrow; nearly 6 times as long as broad at apical ⅓; slightly constricted at middle; but margins essentially subparallel.

Illustrations

103. Spermatheca, genitalia and anal segments
107. Lumacaudate process
108. Processes of clasper

104. Head and prothorax (♂)
105. Lateral metanotal area (♂)
111. Distal arm of sternum 9
113. Apex of aedeagus

Comment. This species, known in Malaya from 11 specimens, was only found in two localities, both in Perak. Eight males were taken at the first area, viz., the limestone forest a few miles west of Ipoh at 1100–1300 ft elevation. The species was collected here only on 4 occasions, always from *Lariscus insignis*, and at times accompanied by *M. dryadosa*, which was more common on these ground-squirrels in the area than was *M. calcarata*. The second area was on Maxwell Hill, Gunong Hijau, 3000–4200 ft elevation, where 3 specimens (1 ♂, 2 ♀) were taken from 2 *Lariscus*. It seems likely that *Lariscus* will prove to be the most common host of this flea. The lack of records of *M. calcarata* in the well studied dipterocarp-forested hills near Kuala Lumpur is notable.

It is of interest that this species apparently occurs in Sarawak as well. Mr Lim Boo Liat collected 19 fleas from *Lariscus* 18 miles south of Kuching, of which 17 were males of the new species next described, 1 ♀ was *M. phangi tana* and 1 ♀ was inseparable from Malayan *calcarata* at the species level, including the long labial palpi and terminal maxillary palpal segment and the internal genitalia, etc.

The name *calcarata* is derived from the Latin term *calcar*, meaning a spur, and refers to the conspicuous spiniforms on the male sternum 9.

9. **Medwayella batibacula** sp. nov.

Type material. Holotype ♂ (B-84199) ex *Lariscus insignis*; EAST MALAYSIA: Sarawak, Kuching, Bukit Stigang, Kampong Pangkalan Kuap; 27.XII.1968; Coll. Lim Boo Liat. Paratypes as follows: 11 ♂ with same data as holotype, but 26–28.XII.1968. 4 ♂ Sarawak, Tijirak, 19 mi S of Kuching; 7–12.I.1969; Coll. Lim Boo Liat. 1 ♂ Sarawak, Pueh; 7.VI.1958; Coll. T. C. Maa. Holotype (U.S.N.M. number 71607) and 1 paratype in U.S. National Museum. Paratypes in collections of Bishop Museum, British Museum (Natural History), the Canadian National Collection (Ottawa) and the author.

Diagnosis. Near *M. calcarata* and agreeing with *M. loncha* in same respects as those cited in the previous description (number 8). Separable from *M. loncha* by at least diagnostic features numbers 1–3 and 5–9 cited for *M. calcarata*. Distinguishable from *M. calcarata* as follows: (1) Labial palpus not extending beyond apex of procoxa instead of reaching tip of trochanter. (2) Segment 4 of maxillary palpus only 1·6 times as long as third, not 1·75 times. (3) Inner dimensions of lateral metanotal area (fig. 106, L.M.) virtually as high as long instead of being definitely longer than high as in *M. calcarata* (fig. 105, L.M.) and *M. dryadosa* (fig. 5). (4) Third vinculum (V.C.3) with dorsal surface sinuate and strongly upcurved at apical ½, the link-plate usually lying at an angle of about 45° except for distal curve into point of articulation in latera metanotal area. In *M. calcarata*, V.C.3 is quite flat dorsally for about ½ its length before curving towards L.M. and its axis is nearly horizontal, much as in *M. dryadosa*. (5) Margin of lobe at cephaloventral corner of mesepisternum virtually truncate instead of definitely sinuate as in the other 2 species (fig. 9, MPS.). (6) With a distinct bulge on ventral margin of manubrium (w in fig. 1, *q.v.* &

cf.) immediately anterior to sinus (v) near basal $\frac{1}{3}$ instead of that region (w) being quite flat (even though sinus may be deep) as in *M. calcarata* and *M. dryadosa* (fig. 18, MB.). (7) Movable finger (fig. 109, F.) with caudal margin somewhat convex proximally, e.g., at point q, at level of apex of conical process (C.P.), instead of quite straight as in *M. calcarata* (fig. 108). (8) Dorsal margin of process of P. quite straight, lacking subapical sinus. (9) D.A.9 (fig. 112) with ventral (caudal) margin (*cf.* fig. 3, qq–u3) curving dorso-apicad at an angle of 45°, commencing just above point q3, somewhat distad of level of subapical lobe (SUB.L.), and resembling a flattened arc. Tip (qq) of apical extension (EXT.9) only slightly upturned. In *M. calcarata* (fig. 111) the dorso-apical curve commences more distad, at level of third spiniform from tip, and apex of EXT.9 is so upcurved that its tip (qq) is at right angles to longitudinal axis of arm. (10) Semimembranous portion of dorsal margin of D.A.9, above apex of supramedial flap (SUP.FL.) arcuate and joining EXT.9 at apex instead of being distally excised. (11) Sub-rhomboidal tanned portion of quasi-crochet (fig. 115, Q.C.) proportionately much longer and narrower, viz., more than twice as long as broad instead of 1·7 times. (12) Apicoventral corner of Q.C. produced into a short nubbin instead of being squared. (13) Body of crochet (B.CR.) much broader subdorsally, its breadth there subequal to maximum breadth of phylax (PHY.) instead of being only $\frac{1}{3}$ that of PHY. (14) Securifer with groove (GRV.) broader at depth of curve than subapically (both dorsally and ventrally); breadth of groove never approaching that of base of upper arm (U.A.) instead of exceeding it throughout. (15) U.A. broad for most its length; length of basal $\frac{1}{2}$ only equal to 2·5 times its breadth instead of more than 4 times. (16) Lower arm (L.A.) of securifer with apical margin angulate, not slightly concave. (17) Phylax (PHY.) proportionately narrower, viz., about 3·4 times as long as broad at maximum level (near base) instead of 2·3 times; its axis sinuate instead of straight for basal $\frac{2}{3}$. (18) Sclerotized inner tube (S.I.T.) with dorsal spur arching dorsad but recurved towards axis of tube; its arc removed from S.I.T by a distance equal to 4–5 times breadth of base of spur. In *M. calcarata* the spur parallels tube for most its length and is close to it, the distance separating them less than twice basal diameter of spur. (19) S.I.T. subapically dilated instead of being of uniform diameter to apex.

(Female unknown)

Descriptive notes. Differences from *M. dryadosa* are also included in the above diagnoses, and additional ones follow. Squamulum horizontal. Sternum 8 with cuadal margin slightly concave except for well rounded corners. Lumacaudate process (fig. 116, LUM.) neither well developed nor demarcated; lobate portion conical, with ventral margin commencing at level of 2 relatively long, stout ventromarginal bristles; length from here twice breadth at midline; with only about 16 close-set bristles, none of which truly spiniform, in 5–6 irregular rows. Movable finger (F.) with a mesal suture running from apex of stiva to middle of tip of F. (fig. 110 and approximating p–n in fig. 1); another mesal seam extending from base of distal fringe (D.FR.) transversely across F. to apical $\frac{1}{3}$ of anterior margin. Distal arm of sternum 9 about 8 times as long (ii–qq) as broad at level (jj–uu) of transverse sclerotization (fig. 112, T.S.). Upper portion (bb–ff) of posterior margin of proximal arm of sternum 9 flat, subparallel to that of anterior margin (aa–dd).

ILLUSTRATIONS

106. Lateral metanotal area (♂)
109. Processes of clasper
110. Mesal aspect of F.
112. Distal arm of sternum 9
115. Apex of aedeagus
116. Lumacaudate process

COMMENT. All of the known specimens, 17 males representing 9 collections, were from *Lariscus insignis* in the same general area and habitat in Sarawak. (Usually female fleas are more common than males, at least in collections, and it is unprecedented to obtain such a large series of males in the absence of females.) The superficial similarity to *M. calcarata* from Perak in Malaya, and which might also be a *Lariscus* flea, is quite striking. The differences apparent on critical study, however, cited above, are too great for subspecies and indicate the two are sibling species. This belief is supported by the fact that a female virtually indistinguishable from Malayan *M. calcarata* was collected from the same host and locality as the type series of *M. batibacula* (along with a single female of *M. phangi*). It is highly unlikely that the ength of the labial palp and all the other significant characters noted would vary only in the Sarawak male, while the female remained unchanged in the course of evolution. It seems most probable that *M. calcarata* occurs both in Sarawak and Malaya, parelleling the distribution of *M. phangi* and *M. robinsoni*. Further collections are urgently required to clarify this point and the many other questions posed by the chronic shortage of specimens of Siphonaptera for study from sundry hosts and habitats throughout most of the Asiatic-Pacific area.

The name *batibacula* is derived from the Latin words for thorn or spine (*batus*) and staff or rod (*baculus*), and the "thorny staff" refers to the distal arm of sternum 9.

10. **Medwayella veruta** sp. nov.

TYPE MATERIAL. Holotype ♂, allotype ♀ (B-19165-1) ex squirrel nest; EAST MALAYSIA; Sabah (N. Borneo), Mt. Kinabalu, Ranau; elev. 1500 ft; 31.VII.1953; Coll. R. Traub. Paratypes as follows: 5 ♂, 3 ♀ with same data as holotype. 2 ♂, 1 ♀ ex *Sundasciurus lowi*; loc. cit., but 13.VII, 6.IX.1953. 1 ♀ ex *Tupaia* sp.; loc. cit., but 2.VIII.1953. 1 ♂ ex *Ptilocercus lowi*; loc. cit., but 13.VII.1953; Coll. R. Traub & H. D. Newson. 2 ♂ ex *Tupaia* sp.; 18 mi S of Tenom Kg Bara Jumpa; 2.II.1963; Coll. J. A. Bullock.

Holotype (U.S.N.M. number 71608) and allotype in U.S. National Museum. Paratypes in British Museum (Natural History) (1 pair) and in author's Collection.

DIAGNOSIS. Agrees with *M. loncha* in the same respects as those listed for *M. calacrata* (*q.v.* number 8) and thereby instantly separable from *M. dryadosa* and allies, while the characteristic shape of D.A.9 of *M. veruta* (fig. 120), *M. batibacula*, etc., readily distinguishes this group from *M. phangi* (fig. 68) and its relatives.

Readily separable from *M. loncha* as follows: (1) Movable finger (fig. 119, F.) not nearly as foreshortened and broad subapically, viz., about 3·75 times as long (s–n in fig. 1, *q.v.* & *cf.*) as broad (j–k) below distal fringe (D.FR.); not merely thrice (fig. 126). (2) Bristles of D.FR. with bases forming an oblique line instead of a straight line paralleling longitudinal axis (s–n) of F. (3) F. with convexity of caudal margin (q) near P. exceeding that of cephalic margin (i) near conical process (C.P.) instead of

being flatter than that of opposite margin. (4) Posterior margin of P. (t–u) somewhat convex below level of subapical long bristle instead of being straight to near sinus (v) near fulcral sclerite (F.S.). (5) Anterior (dorsal) margin of D.A.9 (fig. 120) with portion distad and proximad of spur (SUB.L.) (*cf.* fig. 3, e3–f3 & c3–kk) lying in different planes, D.A.9 being much broader proximad to SUB.L. than distad; instead of anterior margin forming a straight line (kk–qq) interrupted by spur. (6) Distance (e3–qq) from SUB.L. to apex of segment (EXT.9) shorter than in *M. loncha*, e.g., distance (b3–qq) from dorsal (anterior) apex of transverse sclerotization (T.S.) to tip of arm is 3·7 times distance (e3–qq) from upper margin of base of SUB.L. to apex of EXT.9, instead of only 2·7 times. (7) SUB.L. proportionately closer to upper limit of mid-microspiculate area (M.MSP.), viz., distance (c3–kk) between them subequal to length of bristles of caudomarginal submedian group (CM.G.B.) instead of clearly exceeding it. (8) Anterior margin of D.A.9 (e3–qq) extending to apex of arm even though lightly tanned distally, instead of curving caudad subapically (f3). (9) Deltoid flap of aedeagus (fig. 114, DEL.FL.) only twice as tall as long instead of 2·4 times. (10) Tanned portion of quasi-crochet (Q.C.) proportionately longer and narrower, thrice as long as broad at middle instead of 1·3 times. (11) Unique in that phylax (PHY.) is curved caudad apically so that there is a short, broad lobe at dorsocaudal corner. In other *Medwayella* the caudal margin is straight for the upper ½ and hence there is no lobe. (12) Phylax narrower than in *M. loncha* and more constricted subventrally, although both are broadest near middle. Length 3·2 times midgirth, and 4 times that at narrowest point, instead of 2·8 and 3·5 times. (13) Groove (GRV.) of Ford's sclerite widest at middle and narrowest near dorsal apex, instead of vice versa. (14) Upper arm (U.A.) of securifer with dorsal margin sinuate —the trough proximal and height of convexity just apicad of middle, whereas in *M. loncha*, dorsal margin is evenly concave to near apex. (15) Lower arm (L.A.) with upper margin convex or peaked near apex, not fairly straight (though microserrate). (16) Dorsal spur of sclerotized inner tube (S.I.T.) large, sloping cephalodorsad at angle of 60°, then recurved over tube and apex connected with it; resembling a triangle with a hollow center, whose base equals diameter of S.I.T. and whose altitude is about ⅔ that diameter. In *M. loncha* the spur commences more vertically, is apically recurved and presumably lacks elements returning anteriorly to S.I.T. (17) Subventral sinus of ♀ sternum 7 (figs 117, 124) open dorsally, there being no true notch, whereas in *M. loncha* (figs 118, 130) caudal margin above ventral lobe is inclined to an angle of about 60° until near apex of lobe, so that there is a notch. (18) Caudal margin of 7 S. (fig. 124) with a short but distinct median lobe where it recurves cephalodorsad. In *M. loncha* (fig. 130) curve is effected without production of a lobe. (19) Perula of bursa copulatrix (P.B.C.) relatively shorter and broader, viz., only about 2·2 times as long as broad at lower ⅓, instead of 4 times. (20) With a distinct "gland" between glandula vaginalis (G.VG.) and orifice of vagina; this lacking in *M. loncha*.

Descriptive notes. The characters cited above also differentiate *M. veruta* from *M. dryadosa* and additional points follow. Lateral metanotal area with quadrate untanned area taller than long. Squamulum horizontal and more than 5 times as long as broad at middle. Spiracular fossa of metepimere sagittate but with ventral

margin straight and sloping somewhat dorsocaudad; dorsal margin slightly inclined from horizontal for first ½ and then sloping ventrocaudad towards apex; about 1·3 times as long as tall at maximum level. Spiracular fossa on 2 T. 1·6 times as long as broad; 2·3 times on 6 T. Lower antepygidial bristle about 2·5 times length of upper one in male; 2·4 times in female. With dorsal lower modified bristle (fig. 124, L.M.B.) a smaller, thinner version of upper antepygidial bristle; L.M.B.-2 resembling long bristles of adjacent row. Lower lobe of 7 T. (L.L.7) below A.B. blunt.

Male. Ventral extension of 8 SPC. with height subequal to or exceeding diameter of horizontal section. Lumacaudate process (LUM.) with densely bristled area about 2·4 times as long as high; apically broadly or obtusely rounded. Conical process (fig. 119, C.P.) about 5 times as long (e–h) as broad (f–g). Dorsocaudal corner of F. scarcely produced into a snout, e.g., stiva (STV.) poorly developed, in that distance (l–p) from anterior margin near apex (l) to tip of stiva (p) is 6·5 times length of stiva (p–o/k). Distal fringe (D.FR.) consisting of 4 or 5 bristles; lowermost the thinnest. Sinus of ventral margin of manubrium (v) long and shallow; the bulges (u and w) flanking it correspondingly short. Upper sinus (aa–cc) of anterior margin of P.A.9 much deeper than lower sinus (cc–dd), which is virtually flat. D.A.9 about 8 times as long (ii–qq) as tanned region is broad (uu–jj). With about 5 or 6 marginal spiniforms on caudal margin of D.A.9, of which lowest 4 are usually longest and stoutest, and distalmost of long ones generally at level of SUB.L. (d3–q3). Mid-microspiculate area (M.MSP.) highly convex and apically bulging above D.A.9 nearly as much as SUB.L., but cavity of receptacle with D.A.9 correspondingly fairly shallow. Lateral laminae of aedeagus and middle lamina relatively broadly yoked at tip of apex of apodeme, margins of the plates parallel until summit. Sinus of hood (HD.) deeply excised, reaching to near apex of B.CR. Upper margin of deltoid flap (DEL.FL.) evenly but shallowly concave. Vertical portion of phylax (PHY.) slightly sinuate.

Female. Spermatheca (fig. 123) with bulga (B.) bearing a short but distinct peak. Ventral lobe of sternum 7 short and broad; scarcely longer than tall. Anal stylet (fig. 122, A.S.) scarcely narrowed from base to near apex; about 4·6 times as long as broad at middle. Tergum 8 (fig. 125, 8 T.) broadly ovate at ventrocaudal angle, lacking a distinct lobe.

ILLUSTRATIONS

114. Apex of aedeagus
117. Spermatheca and genitalia
119. Processes of clasper
120. Distal arm of sternum 9
121. Sternum 8 (♂)
122. Anal lobes and stylet (♀)
123. Spermatheca
124. Sternum 7 (♀)
125. Genitalia (♀)

COMMENT. As can be seen from the type data, *M. veruta* was found on *Sundasciurus lowi*, on *Tupaia* sp., and in the nests of squirrels on the foothills at the base of Mt. Kinabalu. In addition, the author and H. D. Newson collected a male from a nest, occupied by a pen-tailed shrew (*Ptilocercus lowi*), in a branch in a tree in the same area. It is worthy of note that this species was also collected on *Tupaia tana* in Sarawak, in Division III at Nanga Balleh, near Kapit (R.T.). This constitutes only the second

known instance of a North Bornean indigenous flea occurring in Sarawak (and apparently represents a distinct subspecies). (The other species is *Stivalius mjobergi* Jordan, 1926, described from Mt. Murud, which is just south of the border of N. Borneo.) However, the differences in the Siphonapteran fauna of Sarawak as compared to North Borneo, which superficially appear to be striking, may prove to be more apparent than real when the mountains of Sarawak are studied, and as more of the lower elevations in North Borneo are surveyed. This is discussed further below (Section A.14), and in the third article in the series.

The name *veruta* is a Latin term meaning armed with a spear or javelin and refers to the rod-like extension of the spined distal arm of sternum 9.

11. **Medwayella loncha** (Jordan, 1926) NEW COMBINATION

Stivalius lonchus Jordan, 1926. Novit. zool. 33:390, figs 11, 12; Costa Lima & Hathaway, 1946, Pulgas: 327; Smit, 1958, Bull. Brit. Mus. (Nat. Hist.) Ent. 7(2):3.

To date this species has been known only from the single specimen collected by Dr E. Mjöberg ex *Tupaia* sp. in Sarawak, Mt. Poi, 5000 ft elev. described by Jordan in but 4 lines and illustrated by one figure showing the upper portions of the movable finger and distal arm of sternum 9. The published material is inadequate for recognition of the species, and in fact is misleading, for instead of the movable finger F. being "not essentially different," we now are aware of a sufficient number of species in the group to realize that F. *is* distinctive. The collection of *M. loncha* and the related new species, *M. batibacula*, by Lim Boo Liat in Sarawak, and the discovery of another allied new species, *calcarata*, plus access to the type specimen, have rendered clarification of the characteristics of *M. loncha* possible, as well as description of the hitherto unknown female.

Diagnosis. The salient features of *M. loncha* have been listed in the comparisons made above in the descriptions of the new species *M. calcarata* and *M. veruta*, *q.v.* It is readily recognizable in the ♂ by the relatively short, broad F. (fig. 126), which is scarcely more than thrice as long (from apex of immovable process P., *cf.* fig. 1, n–s) as broad at narrowest level (immediately below level of distal fringe, D.FR., or j–k). It is further characterized by a D.A.9 (fig. 127) bearing a distal, vertical "spur" (EXT.9) instead of being curved to form an apical lobe (*cf.* fig. 20, AP.L.) etc., and by an aedeagus (fig. 128) with a groove (GRV.) between alpha portion (ALPH.) and base of upper arm (U.A.) of securifer. The short, broad quasi-crochet (Q.C.) is diagnostic—region distad of phylax (PHY.) is only 1·3 times as long as broad because of markedly convex dorsal margin (but upper portion lightly tanned). Female distinguishable by the following combination of characters: (1) Sinus of sternum 7 (figs 118, 130, 7 S.) very broad apically, and already diverging markedly from ventral margin at base. (2) Perula of bursa copulatrix (P.B.C.) elongate-ovate, but with anterior margin quite straight. (3) Paragenital morion so lightly tanned as to be virtually inapparent. (4) Lacking a "gland" caudad to glandula vaginalis (G.VG.). (5) Mesal genitalic ridge of tergum 8 (M.R.8) with anterior margin sinuate; subhorizontal fork aborted; anterior branch of fork short and narrow. (6) Ventrocaudal corner of 8 T. with a short, broad lobe.

ILLUSTRATIONS

3. Distal arm of sternum 9
118. Spermatheca and genitalia
126. Processes of clasper
127. Distal arm of sternum 9
128. Apex of aedeagus
129. Sensilium and anal segments (♀)
130. Sternum 7 (♀)
131. Sternum 8 (♂)
132. Spermatheca

RECORDS. 2 ♂, 1 ♀ ex *Sundasciurus lowi;* EAST MALAYSIA: Sarawak, Tijirak, 19 mi S of Kuching; 28–30.XII.1968; Coll. Lim Boo Liat. 1 ♂, 1 ♀ ex *Tupaia tana*; loc. cit.; 26.XII.1968.

COMMENT. It seems significant that this species was collected only on *Sundasciurus* and *Tupaia* but not on *Lariscus* in the same area, and that the latter were parasitized by *M. batibacula*. The material herein described and figured as *M. loncha* agrees closely with the type specimen in the British Museum.

12. **Medwayella javana** (Jordan, 1933) NEW COMBINATION

Stivalius javanus Jordan, 1933, Novit. zool. 38:355–356, figs 76, 77; Costa Lima & Hathaway, 1946, Pulgas: 327; Smit, 1958, Bull. Brit. Mus. (Nat. Hist.) Ent. 7(2): 3.

Another species known heretofore only from a single ♂ (and 3 ♀), *M. javana* was described from specimens collected from *Tupaia javanica occidentalis* (holotype ♂), "*Rattus bukit temmincki*" (probably *R. fulvescens temmincki*) (2 ♀), and *Callosciurus n. nigrovittatus* (1 ♀) at "Tjiboeni, Bandong, W. Java" (today known as Tjibuni, Bandung). The present descriptive notes and illustrations are based upon a pair collected from *Tupaia javanica* by J. M. Stusak of the B. P. Bishop Museum, 30.IX. 1965 at Tjibodas, Java, 5200 ft elev., and which agree quite closely with the original description and photographs of the type material.

DIAGNOSIS. Some cardinal characters have already been noted in the description of *M. arcuata, q.v.* Salient points are: (1) Distinctive amongst known *Medwayella* in that the movable finger (fig. 133, F.) is long and narrow, viz., portion distad of apex of immovable process P. (*cf.* fig. 1, r–n) is about 4 times as broad at level of apex of conical process (i–q) and 5 times as long as broad at middle of subapical constriction (j–k). (2) The only other species besides *M. arcuata* in which dorsal margin of distal arm of sternum 9 (fig. 124) is deeply arcuate subapically (ARC.) instead of either bearing a true notch (figs 20, 21) or being homolate (figs 68, 81). In *M. javana*, ARC. is fairly shallow, i.e., 5 times as long (*cf.* fig. 1, mm–pp) as deep at trough. (3) Apical lobe (AP.L.) extending more dorsad (cephalad) than subapical lobe (SUB.L.). (4) Aedeagus (figs 95, 96) of the *M. robinsoni* type in that thumb (THM.)is in the "cocked" position and lower arm (L.A.) of securifer is broad and apically blunt, not acuminate. (5) Height of THM. slightly less than breadth of apex. (6) Upper arm (U.A.) of securifer distally acute but broad to basal half. (7) L.A. with lower margin about 1·8 times as long (from edge of body of crochet, B.CR.) as broad at middle; dorsal margin angulate and sloping from middle towards ventrocaudal corner at angle of about 45°. (8) Tanned portion of quasi-crochet (Q.C.) fairly short and broad, about 2·6 times as long (from edge of phylax, PHY.) as broad at middle; subapically somewhat dilated and apex obtuse. (9) Sclerotized inner tube (S.I.T.) well upcurved

beyond level of long, straight dorsal spur. (10) Lumacaudate process (fig. 135) well defined; narrow—with only 1 spiniform bristle at apex and no more than 3 or 4 per row in breadth; length (from anterior spiniform) about 1·75 times breadth at middle. (11) Sternum 7 of ♀ (fig. 40, 7 S.) unusual in that ventrocaudal lobe is sinuate apically. (12) Ventrocaudal sinus of 7 S. short, dilated apically. (13) Perula of bursa copulatrix (P.B.C.) pyriform, with expanded portion ventral, but anterior margin quite flat. (14) Paragenital morion (PG.M.) with a conspicuous tanned rod-like element buttressing P.B.C. (15) Mesal genital ridge of tergum 8 (M.R.8) with anterior and median margins sinuate; lower branch below fork short, thin and lightly tanned. (16) Caudoventral lobe of 8 T. fairly short, broad at base and with an angle of about 35° at tip. (17) With glandula vaginalis (G.VG.) long and thin; no other "glands" caudad of it.

ILLUSTRATIONS

40. Genitalia (♀)
95. Apex of aedeagus
96. Sclerotized inner tube
133. Processes of clasper
134. Distal arm of sternum 9
135. Lumacaudate process
136. Sternum 7 (♀)
137. Spermatheca, genitalia and anal segments

13. **Medwayella rhaeba** (Jordan, 1926) NEW COMBINATION

Stivalius rhaebus Jordan, 1926, Novit. zool. 33:389, figs 9, 10; Jordan & Rothschild, 1926, Sarawak Mus. Jour. 3 (part III) (10): 290, figs 6, 7; Costa Lima & Hathaway, 1946, Pulgas : 327; Smit, 1958, Bull. Brit. Mus. (Nat. Hist.) Ent. 7(2) : 3.

This species is still known only from the single pair from "*Sciurus brooksi*" (*lapsus* for the squirrel now called *Sundasciurus brookei*) on Mt. Dulit (Sarawak) and from the abbreviated descriptions and figures by Jordan in 1926 and Jordan & Rothschild in 1926. The diagnostic features mentioned in the present article are based primarily upon photographs of the holotype (♂) and allotype in the British Museum.

DIAGNOSIS. Apparently unlike any of the other described species in the shape of the movable finger (fig. 138, F.). At level of base of crochet process (CR.P.), breadth of F. exceeds that at apex, yet narrowed to half that breadth at apical third (measuring from base of CR.P. or summit of immovable process P.). F. rapidly broadening above that level, largely due to oblique caudal margin slanting at 45° to tip of stiva. Distal fringe (D.FR.) of 3 stout bristles inserted immediately below apex of stiva. Distal arm of sternum 9 (D.A.9) diagnostic by virtue of denticulate tip or nubbin at anterodorsal angle. Other characteristics are mentioned in comparisons made with *M. phangi* (number 5 above). The heavily sclerotized, arched, horizontal section of the mesal genitalic ridge of ♀ sternum 8 (fig. 139, M.R.8) seems to be unique amongst known *Medwayella*.

M. rhaeba agrees with *M. phangi* in being a species with a grooved Ford's sclerite (GRV.), with a narrow, upturned quasi-crochet (Q.C.) and with a homolate D.A.9 (*cf.* figs 68, 71, *M. phangi*). However, the differences are striking, as has been pointed out above.

ILLUSTRATIONS

138. Modified abdominal segments (♂)
139. Modified abdominal segments (♀)

14. GEOGRAPHIC AND HOST-DISTRIBUTION OF MEDWAYELLA IN MALAYA

A consideration of the ecological, geographic and host-distribution of *Medwayella* is worthwhile even though virtually nothing is known about the flea-fauna of the eastern districts of the Indian subcontinent (such as Assam, Manipur, the Chittagong Hills, etc.) and of the bulk of the Indonesian Archipelago (i.e., except Sumatra and Java, for which we have sparse information) and despite the fact that data are minimal for the northern and eastern parts of the Indo-China subregion.[6] Thus, even though collections from the peripheral regions of the range for *Medwayella* are sorely needed, it is possible to make some generalizations which seem significant. The zoogeographical observations and implications in the main are discussed in the third article in the series, and what follows here will largely deal with the types of hosts infested and where they were found.

Thirteen species of *Medwayella* are mentioned in this paper. Six of these are known from Sarawak, five from Malaya, two from Sumatra, two from Thailand and one each from Sabah (N. Borneo), Java and Indo-China. Of the 13, *M. robinsoni* is known from four of the areas listed (Malaya, Java, Sarawak and Thailand), and two species (*M. calcarata* and *M. phangi*) occur in both Sarawak and Malaya. (The fact that some are found in several countries, of course, meant that the numbers just cited will add up to more than 13.) This recorded distribution, to a great extent, reflects the degree of collecting done per area, but even so, certain trends suggested by the data are valid. Thus, while as yet undescribed species undoubtedly exist in Indonesia, and two such are known from the Philippines, and the genus probably occurs in eastern India and Burma, sufficient field-work has been done in Indo-China and Thailand to show that the number of endemic species of *Medwayella* is well below that for Malaya and Borneo, which seem to be the center of development of the genus.

Of the countries mentioned, the only one for which there are sufficient data for detailed discussion of hosts and distribution in Malaya, and the available records are summarized in Tables 1 to 6. (It is reiterated that the numbers of hosts cited in Table 2 as having been examined includes only our own collections, and thus these do not represent the hosts trapped or shot by our colleagues in Kuala Lumpur. The numbers of fleas, however, do include all available specimens.)

The sciurids listed as tree-squirrels (T) in Table 2 are essentially arboreal and nest high in the trees, but do come to the ground on occasion. The ground-squirrels and ground-dwelling forest-rats (marked G) spend most of their time on the forest-floor

[6] It should be noted that the geographic names and expressions used in this article are those that have a fairly specific connotation in zoogeography, history or usage. Thus, there are no political considerations in the term "Indo-China," which is an established name for a zoogeographical subregion. Similarly, to a naturalist, "Malaysian" includes lower Burma and some of the Indonesian Islands, and hence this term has been avoided when speaking of the country formerly called Malaya, or of the part of Borneo previously under British rule. The expression "Malayan" as used here, refers to the Peninsula and does not have the zoogeographic connotation of a Malayan (or Malaysian) subregion.

TABLE 2

HOST-DISTRIBUTION OF FIVE *MEDWAYELLA* FLEAS ON THE MALAYAN PENINSULA

Hosts			Fleas—Numbers and percentages of *Medwayella* species										
		Minimum Number	*dryadosa*		*phangi*		*limi*		*calcarata*		*robinsoni*		
Name	Habits	Exam'd	No.	%	No.	%	No.	%	No.	%	No.	%	Totals
1. *Callosciurus caniceps*	T	184	–	–	–	–	1	3%	–	–	92	9%	93
2. *Callosciurus erythraeus*	T	38	–	–	–	–	–	–	–	–	6	•	6
3. *Callosciurus nigrovittatus*	T	110	–	–	–	–	–	–	–	–	139	14%	139
4. *Callosciurus notatus*	T	259	–	–	2	3%	–	–	–	–	206	20%	208
5. *Callosciurus prevosti*	T	18	–	–	–	–	–	–	–	–	4	•	4
6. *Sundasciurus hippurus*	T	23	–	–	–	–	–	–	–	–	28	3%	28
7. (Arboreal Squirrel Nest)	(T)	6	–	–	–	–	–	–	–	–	32	3%	32
8. *Sundasciurus tenuis* & *S. lowi*	T + G	348	1	•	27	39%	–	–	–	–	212	21%	240
9. *Tamiops macclellandi*	T + G	45	1	•	–	–	–	–	–	–	4	•	5
10. *Tupaia glis*	T + G	211	12	9%	33	49%	1	3%	–	–	193	19%	239
11. *Tupaia minor*	T + G	36	–	–	1	1·5%	–	–	–	–	9	•	10
12. Forest Rats (Scansorial)	T + G	117	–	–	–	–	1	3%	–	–	32	3%	33
13. Forest Rats (Ground)	G	362	7	5%	1	1·5%	–	–	–	–	11	1%	19
14. *Dremomys rufigenis*	G	74	3	2%	–	–	–	–	–	–	6	•	9
15. *Lariscus insignis*	G	52	20	15%	4	6%	3	7%	11	100%	9	•	47
16. *Rhinosciurus laticaudatus*	G	23	85	65%	–	–	36	84%	–	–	12	1%	133
17. (Other)	–	102	1	•	–	–	–	–	–	–	15	1%	16
Totals			130	±100%	69	100%	42	100%	11	100%	1010	±100%	1261

T = Tree-dwelling G = Ground-dwelling • = less than 1%

and nest below the surface, as amongst the roots of trees, but at times climb on tree-trunks and low trees and shrubs. *Tupaia* are active on the ground and are also at home on trees, at least on lower limbs. Their common name, tree-shrew, therefore is at least partially correct (since most mammalogists no longer regard them as shrews). The *Tupaia* and the scansorial forest-rats and the squirrels like *Sundasciurus tenuis*, *S. lowi* and *Tamiops maclellandi*, which can be seen and/or collected both on trees and the forest-floor, are designated as "T + G," for "tree and ground." Flying-squirrels, e.g., *Petaurista* and the giant tree-squirrel, *Ratufa*, were collected too seldom for discussion, but no characteristic species of fleas have been found on the 15–20 specimens of each examined by me in Malaya, while "strays" like *M. robinsoni* were rare. (It is interesting that in the Himalayas, *Petaurista* and *Hylopetes* flying-squirrels are infested with several fairly specific genera and species of fleas of Indo-Malaysian affinity and that in Formosa *Petaurista* regularly bears fleas, but of a palearctic species. An endemic genus has also been found on *Hylopetes* in N. Borneo.)

Several points are readily apparent from the data in Table 2. For example, of the five species listed, only *M. robinsoni* has been taken with any frequency on *Callosciu-*

TABLE 3

HOST-DISTRIBUTION OF FIVE SPECIES OF *MEDWAYELLA* FLEAS ON THE MALAYAN PENINSULA (SUMMARY)

HOST	SPECIES OF MEDWAYELLA				
	DRYADOSA	PHANGI	LIMI	CALCARATA	ROBINSONI
I. ARBOREAL SQUIRRELS		3%	2%		49%
II. SEMI-ARBOREAL AND GROUND-SQUIRRELS	85%	46%	93%	100%	25%
III. TUPAIA	10%	50%	2%		21%
IV. FOREST-RATS	5%	1%	2%		4%
TOTAL %	100%	100%	±100%	100%	±100%
TOTAL NUMBER OF FLEAS	129	68	42	11	963

rus, a genus of tree-squirrels. In fact, of the remaining four species, only *M. phangi* and *M. limi* were ever collected on an arboreal squirrel and then only once each, i.e., two of the former from *C. notatus* and one from *C. caniceps* for the latter. In contrast, 65% of the records for *M. dryadosa* and 84% of those for *M. limi* were from *Rhinosciurus laticaudatus*, a ground-squirrel. Nearly half of the *M. p. phangi* were collected on the tree-shrew, *Tupaia glis*, but 39% were from the small *Sundasciurus* squirrels, which are frequently on the forest-floor. The second most prevalent host for *M. dryadosa* was the ground-squirrel, *Lariscus insignis*, accounting for 15% of those collected. All of the known Malayan *M. calcarata* likewise were from that host. However, the numbers involved (11 specimens) are too low for certainty regarding host-specificity of *M. calcarata*, although they represent seven different collections.

The apparent dearth of *Medwayella* reported from the ground-squirrel *Dremomys* seems noteworthy, but is misleading in a sense, since this squirrel is montane and the *Medwayella* being discussed are rare or absent above 4000–5000 ft. The host-range of *M. robinsoni* is obviously far greater than for other members of the genus, e.g., it was collected at least once on each type of host. The highest percentages, however, are for the arboreal and the partially arboreal squirrels, rats and tree-shrews.

These data are summarized in Table 3 below, which compares the numbers and percentages of these fleas which were from arboreal squirrels with those from squirrels that divide their time between trees and the ground, and with those from *Tupaia* and rats. From this table, it can be seen that 100% of *M. dryadosa* were from non-arboreal species (accounting for the name of "hater of tree-dwellers"), and that this same tendency was exhibited for *M. p. phangi* and *M. limi* (97% and 98% from ground-dwelling or semi-arboreal hosts respectively). The tree-shrews, *Tupaia*, were "good" hosts for at least three of the five species, particularly *M. phangi* and *M. robinsoni*. Various species of forest-rats, such as the scansorial *Rattus* (*Lenothrix*) *canus* and *R.* (*Maxomys*) *cremoriventer* and the ground-dwelling *R.* (*Lenothrix*) *rajah*, *R.* (*Leopoldamys*) *sabanus* and *R.* (*Stenomys*) *bowersi* at times carried one or two *Medwayella* fleas, generally *M. robinsoni*, but occasionally *M. dryadosa*, and rarely one of the others.

When discussing host-relationships, it is always important to consider infestation-rates. Unfortunately, the data here have limitations, even though for our own collections we have records of the numbers of animals which had no fleas at the time of examination. As mentioned above, since the collections were made to obtain living mammals for studies on scrub typhus, etc., many of the rats had been in the traps for hours, or even more than a day, before being placed in a bag for subsequent examination. Such excited hosts, perhaps drenched by rain, soon lose their fleas, while the ubiquitous and innumerable ants promptly ruin mammals killed by other types of traps. Under such condition, it is impossible to obtain reliable "flea-indices" or infestation-rates, and it is not surprising that the average number of *Medwayella* fleas per mammal in the tables above at times would be less than one, even if the "minimum number examined" were the actual total number. However, it is important to note that nearly all of the tree-squirrels and many of the *Tupaia* and ground-squirrels had been collected by shooting and the specimens were then immediately bagged. Even so, the over-all index was frequently below one flea per host, though

an occasional squirrel would have as many as six or even ten *Medwayella*. No pattern could be determined for the marked variations in numbers noted for squirrels shot in the same locality and on the same day, although I suspect that factors such as sex (lactating females versus males, for example), age, season, etc., all play a role. More data are required in this regard.

Some idea of the infestation-rate can be obtained from the "collection rate" or the number of times the particular fleas were collected from a specific type of host (e.g., the numbers of hosts "positive" for that species of flea). These data are shown, where significant or relevant, for the four new species of *Medwayella* and for *M. robinsoni* (Table 4). These figures also are valuable because they offset the skewing effect of a single unusually large collection, which, while unrepresentative, may exert considerable influence on the mean or total number reported.

TABLE 4

THE NUMBERS OF SPECIMENS OF CERTAIN SPECIES OF *MEDWAYELLA* AND THE NUMBER OF TIMES THESE SPECIES WERE COLLECTED FROM SPECIFIC HOSTS IN MALAYA

Host	Species of *Medwayella*									
	dryadosa		*phangi*		*limi*		*calcarata*		*robinsoni*	
	Fleas	Coll'ns	Fleas	Coll'ns	Fleas	Coll'ns	Fleas	Coll'ns	Fleas	Coll'ns
Sundasciurus tenuis & *S. lowi*	1	1	27	13	–	–	–	–	212	113
Lariscus insignis	20	16	4	4	3	3	11	7	9	6
Rhinosciurus laticaudatus	85	26	–	–	36	15	–	–	12	9
Tupaia glis	12	8	33	18	1	1	–	–	193	82

The data suggest that the indicated association between *M. phangi* and *Sundasciurus tenuis* and *S. lowi* is a fairly close one, since this species was collected from those squirrels on 13 different occasions, even though the total number (27) is small. The same seems true for *M. robinsoni* on these hosts. *M. dryadosa* was relatively frequently taken on *L. insignis* and *Tupaia*, but in small numbers, whereas in the case of *Rhinosciurus*, the average infestation rate was over three (26 collections totalling 85 fleas). The facts that *M. calcarata* was collected from *Lariscus* on seven different occasions (with a total of 11 fleas) and was never taken on another host, suggest an intimate relationship, but additional data are required for verification of this point.

Thus far we have been dealing with *Medwayella* fleas and reported collections from sundry hosts. It is also worthwhile to consider the data from the converse view, viz., the major hosts and the relative numbers of *Medwayella* with which each kind was infested. This is shown in Table 5, whence it can be seen that virtually all the fleas taken on each of the three species of *Callosciurus* were *M. robinsoni*, and that 80% or more of the fleas from *Tupaia* and forest rats belonged to this species. *Lariscus* was most apt to be infested with *M. dryadosa*, although all five species were found on this host at one time or another. Of the 133 fleas reported for *Rhinosciurus*, 64% were *M. dryadosa* and 27% *M. limi*. The absence of *M. phangi* on this host is quite striking, particularly in view of the fact (mentioned below) that *M. phangi* was collected in areas where this ground-squirrel occurred.

Table 5

THE MAIN HOSTS OF *MEDWAYELLA* FLEAS IN MALAYA AND THE RELATIVE PERCENTAGES PER SPECIES WITH WHICH THEY WERE INFESTED

SPECIES OF MEDWAYELLA	CALLOSCIURUS			TUPAIA GLIS	FOREST RATS	LARISCUS INSIGNIS	RHINOSCIURUS LATICAUDATUS
	CANICEPS	NIGROVITTATUS	NOTATUS				
DRYADOSA				5%	13%	43%	64%
PHANGI			1%	14%	2%	9%	
LIMI	1%			•	2%	6%	27%
CALCARATA						23%	
ROBINSONI	99%	100%	99%	80%	83%	19%	9%
TOTAL %	100%	100%	100%	100%	100%	100%	100%
TOTAL NO. OF FLEAS	93	140	208	239	52	47	133

• = less than 1%

The major collecting-localities in Malaya are shown in Table 6, while comments on the habitats in the area have been presented above (p. 207). It is apparent at a glance that *M. robinsoni* was found in all of the regions surveyed, and common in those wherein sufficient material had been collected. In all probability, this species will prove to be abundant in the little-studied Kelantan area and all other *inland* habitats below 4500 ft elevation where *Callosciurus* occurs.

As previously mentioned, we have never collected indigenous fleas along the coastal areas of Malaya (nor along the coast of any other humid tropical country), despite fairly intensive search in some regions, and the presence of species of hosts like *C. caniceps*, *Tupaia*, *R. sabanus*, etc., which carry fleas when farther inland. Indigenous fleas have not been collected on the Sembilan Islands, Pangkor Island and the Langkawi Islands. However, the rodent fauna varies on those islands—only rats occur on the first-named, and rats and tree-shrews are present on Pangkor, while on Langkawi *C. caniceps* was the only squirrel noted, but tree-shrews and sundry forest-rats were found to be plentiful. It is my belief that it is too warm and humid for fleas (or,

TABLE 6

RELATIVE ABUNDANCE OF SPECIES OF *MEDWAYELLA* IN MAJOR COLLECTING-AREAS IN MALAYAN PENINSULA

Species of *Medwayella*	1. Kuala Lumpur Forest	2. Subang Forest	3. Ipoh Hills	4. Gunong Benom	5. E. Coast Forest	6. Kelantan Forest	7. Mountains	8. Kedah
dryadosa	**	*	*	**	⊕	⊕	*	*
phangi	R	**	**	–	–	–	@	**
limi	**	–	–	–	**	–	–	–
calcarata	–	–	*	–	–	–	–	–
robinsoni	***	**	**	**	**	*	*	**

*** = Prevalent ** = Fairly Common * = Occasionally Collected
⊕ = Present, but data inadequate R = Rarely Taken @ = Collected on Kedah Peak

probably, their larvae) in such habitats, but the apparent absence of fleas on Langkawi at 2000 ft elevation is somewhat surprising, and further investigations are desirable to obtain better data in this regard, since we only examined a few rats taken at that height. The fact that *M. robinsoni* and *M. dryadosa* occur on Tioman Island off the east coast, is probably due to the presence of a monsoon season there, which may create favorable conditions for fleas in the dry spell. If so, then *M. robinsoni* may also prove to be present in the northeast coastal region of Malaya, where the climate is also somewhat different from that associated with the typical rainforests of that country.

As for the altitudinal range of *M. robinsoni*, it has been mentioned above that we have a few records of this species occurring (on *C. caniceps*) as high as 5000 ft, at the edge of montane forest, but their presence at such climes seems to be exceptional. Other species of fleas, especially the genus *Macrostylophora* Ewing, 1929, seem to be more characteristic of the higher altitudes, where *Callosciurus erythraeus* is the most abundant tree-squirrel and *Dremomys* the prevalent ground-squirrel. At the other extreme, *M. robinsoni* has been found on squirrels in inland forest only 50 ft above sea-level.

M. dryadosa is another species that was also taken in all of the localities listed in Table 6, although it never was collected as frequently as *M. robinsoni*, probably because its main host, viz., ground-squirrels like *Rhinosciurus* and *Lariscus*, are more difficult to trap or shoot than are *Tupaia* and *Callosciurus*. It seems to be most prevalent in relatively undisturbed dipterocarp forest in the foothills, as at Ulu Gombak, Ulu Langat, etc., in Selangor and at Gunong Benom, rather than in the limestone hills of Perak, the montane forest, or in the lowland, highly modified forest of Subang.

The distribution of *M. phangi* is quite different, although it too ranges widely over Malaya. It was rarely noted in the dipterocarp forest in the foothills of Selangor, and then only at the extreme edges, which has been secondary forest for several decades. In contrast, it was quite common in the highly disturbed forest at Subang (400–700 ft elev.), in the limestone hills of Perak (150–250 ft elev.), at Kedah Peak and at Bukit Wang Forest Reserve in Kedah. The occurrence of *M. phangi* on

Kedah Peak, in contrast to the other mountains studied, is of interest and is commented on below. The fact that 50% of the specimens came from *Tupaia* and 39% from *Sundasciurus tenuis* and *S. lowi* is in accord with this belief that *M. phangi* is associated with secondary forest. The absence of records of *M. phangi* from *Rhinosciurus* is noteworthy, and suggests that this ground-squirrel is primarily a denizen of undisturbed forest, an impression that is heightened by the numbers of collections of *M. limi* and *M. dryadosa* from this host. In this regard it is worth noting that the only area besides the dipterocarp forest near Kuala Lumpur where *M. limi* was found was in the forests of Trengganu, at Bukit Besi, near the east coast.

Although the zoogeography of *Medwayella* and other fleas will be discussed in the third paper in this series, attention is now called to the odd distributional pattern exhibited by some species of *Medwayella*. Three of the species, *M. phangi*, *M. calcarata* and *M. robinsoni*, are known from both Malaya and Borneo, but, in each case, only from Sarawak, not North Borneo (Sabah). Further, two of these have been found only in the western part of Malaya and are common in the Perak-Kedah regions.

15. Key to the known species and subspecies of MEDWAYELLA[7]

1 Labial palpus long, extending to apex of fore-trochanter (fig. 104). Distal segment of maxillary palpus unusually long, 1·75 times length of third segment. ♂ with 3 "supernumerary" bristles (SY.) between rows II and III on head; ♀ with 1 such ***calcarata*** sp. nov. (p. 247)

– Labial palpus shorter, extending generally only to or near apex of procoxa (fig. 4), rarely to middle of fore-trochanter. Distal segments of maxillary palpus only 1·5 times length of third segment. ♂ with 1 supernumerary bristle (SY. and fig. 2); ♀ generally with none 2

2 Males 3

– Females[8] 18

3 Distal arm of sternum 9 (figs 20, 21, D.A.9) with a distinct subapical notch (NCH.) on anterior (dorsal) margin 4

– D.A.9 lacking distinct subapical notch; instead, anterior margin flat between apex and subapical lobe (figs 67, 112, SUB.L.) or else arcuate (fig. 33, ARC.) . . 9

4 Ford's sclerite of aedeagus with a thumb-like process (figs 42, 44, THM.) on alpha-portion (ALPH.) which extends well above base of upper arm (U.A.) of securifer. Upright portion of ALPH. much broader for ventral ⅔ than subapically . . 5

– Ford's sclerite lacking thumb-like process of alpha-portion (fig. 45, ALPH.); apex of ALPH. in line with base of upper arm (U.A.) of securifer. Upright portion of ALPH. rod-like . . . . . ***angustata*** sp. nov (p. 227)

5 Margins of apical lobe of D.A.9 (fig. 20, AP.L.) truncate. Thumb (figs 22, 42, THM.) about thrice as long (tall) as broad . . . . ***dryadosa*** sp. nov. (p. 215)

– Margin of apical lobe of sternum 9 (figs 53–55, AP.L.) angled or with upper half convex. Thumb (figs 56–58, THM.) only 1·2 times (or less) as tall as broad ***robinsoni*** subspp. 6

6 Upper ½ of margin of apical lobe (figs 21, 55, AP.L.) of D.A.9 distinctly convex. Notch (NCH.) with lower margin 1·5–2 times as long as upper margin . . 7

[7] Only one of the alternates cited need apply; these are not combined characters.
[8] The females of *M. rhaeba* (Jordan, 1926) and *M. batibacula* sp. nov. are unknown.

– Upper ½ of margin of apical lobe (figs 53–54, AP.L.) of D.A.9 quite straight or only slightly convex. Notch (NCH.) with lower margin only slgihtly longer than upper margin 8

7 Lower ½ of apical lobe (fig. 21, AP.L.) concave. Lower arm of securifer (figs 23, 44, L.A.) with apex not relatively acuminate; its caudal margin quite straight to near apex. Tanned portion of quasi-crochet (Q.C.) about 4 times as long as broad at middle. (Malayan peninsula) . . ***robinsoni robinsoni*** (Roths., 1905) (p. 233)

– Lower ½ of apical lobe (fig. 55, AP.L.) almost straight. Lower arm of securifer (fig. 57, L.A.) with apex somewhat acuminate due to subventral curve of caudal margin. Tanned portion of quasi-crochet (Q.C.) 3·5 times as long as broad at middle. (Sarawak) . . . . ***robinsoni peregrinata*** snbsp. nov. (p. 234)

8 Upper arm of securifer (fig. 58, U.A.) with apical snout relatively broad, about 2·5 times as long (from vertical internal root) as broad at middle; diameter at middle nearly as broad as subapical portion of lumen of sclerotized inner tube (S.I.T.). Margin of apical lobe (fig. 54, AP.L.) of D.A.9 quite flat and evenly angled at middle. (Java) . . . . . ***robinsoni bogora*** subsp. nov. (p. 235)

– Upper arm of securifer (fig. 56, U.A.) with snout comparatively narrow, about 3–4 times as long as broad near middle; its diameter at middle much narrower than subapical lumen of S.I.T. Apical lobe (fig. 53, AP.L.) of D.A.9 with lower ½ of margin slightly concave; the angle at middle blunt. (Tioman Island, Malaya) ***robinsoni tiomanica*** subsp. nov. (p. 236)

9 Ford's sclerite of aedeagus with a distinct groove (figs 71, 113, GRV.) between alpha-portion (ALPH.) and securifer; but lacking a thumb-like apex to ALPH. Anterior margin of D.A.9 flat immediately above base of subapical lobe (figs 67–68, 111-112, SUB.L.) 10

– Ford's sclerite lacking a distinct groove (figs 94–95, 97–98); thumb (THM.) well developed instead. Anterior margin of D.A.9 arcuate (figs 33, 91, 134, ARC.) above base of subapical lobe (SUB.L.), the arc extending for at least ⅓ length of margin above SUB.L. 16

10 Movable finger (fig. 138, F.) with breadth of subapical constricted area less than ½ that of very broad base and equally broad apex. D.A.9 with a delimited nubbin at anterodorsal angle . . . . . ***rhaeba*** (Jordan, 1926) (p. 257)

– Movable finger (figs 67, 109, 119, F.) with constricted area not as narrowed; always much broader than ½ breadth of apex and generally so for base. Lacking a distinct nubbin at anterodorsal angle of D.A.9, although apex may be pointed (figs 67, 111, 127) 11

11 Caudal margin of D.A.9 heavily sclerotized and apically appearing as a rod-like extension (figs 112, 120, EXT.9); opposite margin lightly tanned. Spiniforms of D.A.9 relatively long and narrow, well spaced. Subapical lobe (SUB.L.) of D.A.9 spur-like. Distal ⅓ of quasi-crochet not appreciably narrower than basal part (figs 114, 128, Q.C.) 12

– Caudal margin of D.A.9 curving subapically (figs 67, 81) and hence not rod-like; not heavily sclerotized; anterior margin tanned to apex. Spiniforms of D.A.9 short and at times close-set. Subapical lobe (SUB.L.) broadly triangular and apex blunt. Distal ⅓ of quasi-crochet much narrower than basal portion, appearing like a tongue-like extension (figs 71, 82, Q.C.) 14

12 Movable finger (fig. 126, F.) short and broad, scarcely more than thrice as long (above apex of immovable process, P.) as broad at narrowest level (immediately below distal fringe (D.FR.)). Relatively tanned portion of quasi-crochet (fig. 128, Q.C.) short and broad, only 1·3 times as long as broad because of markedly convex dorsal margin . . . . . ***loncha*** (Jordan, 1926) (p. 255)

– Movable finger (figs 109, 119, F.) at least 3·75 times as long as broad at narrowest level. Tanned portion of quasi-crochet (figs 114, 115, Q.C.) at least twice as long as broad 13

13 Movable finger (fig. 109, F.) relatively broad throughout, about 3·75 times as long as broad below distal fringe (D.FR.). Tanned portion of quasi-crochet (fig. 115, Q.C.) nearly straight, not angled upwards (but slightly curved)
batibacula sp. nov. (p. 250)

– Movable finger (fig. 119, F.) much broader basally than at constricted area below D.FR.; about 5 times as long as broad at constriction. Quasi-crochet (fig. 114, Q.C.) angled at middle so that distal ½ is at an angle of about 40° with proximal
veruta sp. nov. (p. 252)

14 Movable finger (figs 65, 66, F.) with caudal margin somewhat excised immediately below distal fringe (D.FR.) so that apical portion of F. appears almost stalked. Bases of D.FR. forming a line that is almost perpendicular. Groove of Ford's sclerite extending dorsad together, of equal length (fig. 71, GRV.)
phangi sp. nov. & subsp. nov. 15

– Movable finger (fig. 80, F.) with caudal margin evenly and slightly concave below distal fringe (D.FR.); apical portion of F. not differentiated. Bases of D.FR. forming a markedly oblique line. Groove of Ford's sclerite (fig. 82, GRV.) incomplete dorsally, margin of alpha-portion (ALPH.) extending more distad (dorsad) than opposite member and then forming a characteristic, broad truncate flap . . . . . ***limi*** sp. nov. (p. 242)

15 Movable finger (fig. 65, F.) relatively narrow and arched, so that distal fringe (D.FR.) is on a short stalk. Breadth of F. at constriction much shorter than distance between proximal-most bristle of D.FR. and apex of F. Tip of subapical lobe of D.A.9 (fig. 67, SUB.L.) much closer to dorsal margin of median microspiculose area (M.MSP.) than to apex of D.A.9. (Sarawak) ***phangi tana*** subsp. nov. (p. 242)

– Movable finger (fig. 66, F.) with distal fringe (D.FR.) not on a short stalk. Breadth of F. at constriction subequal to distance between basal bristle of D.FR. and apex of F. Tip of SUB.L. further removed from apex of median microspiculose area (M.MSP.), distance only slightly less than that between SUB.L. and apex of D.A.9
phangi phangi sp. nov. (p. 240)

16 Movable finger long and evenly narrow (fig. 133, F.) about 5 times as long (distad of apex of immovable process, P.) as broad immediately below distal fringe (D.FR.); caudal margin straight near base so that F. is 4 times as long as broad at level of apex of conical process (C.P.). Quasi-crochet with sclerotized portion (fig. 95, Q.C.) relatively short and broad, about 2·6 times as long as broad at middle
javana (Jordan, 1933) (p. 256)

– Movable finger (figs. 34, 92, F.) much broader in proportion and caudal margin markedly bulging near level of conical process (C.P.); at most, scarcely more than 4 times as long as broad below distal fringe (D.FR.) and 2·4 times as long as broad at level of apex of C.P. Tanned, dark portion of Q.C. long and narrow, at least thrice as long as broad at middle (figs 97, 98) 17

17 D.A.9 (fig. 33) with a deep, symmetrical arcuate sinus (ARC.) extending from tip of subapical lobe (SUB.L.) to apex of apical lobe (AP.L.). Ford's sclerite with thumb (fig. 98, THM.) short in height, broader than high. Lower arm (L.A.) of securifer terminating in a short, angulate tip . . . ***arcuata*** sp. nov. (p. 227)

. D.A.9 (fig. 91) with arc (ARC.) above subapical lobe short and shallow, almost indistinguishably merging with apical lobe (AP.L.) so that entire apical region truncate,not lobate, on anterior margin. Ford's sclerite with thumb (fig. 97, THM.) about twice as high as long. Lower arm (L.A.) of securifer with apex acuminate
thurmani sp. nov. (p. 244)

18 Mesal genitalic ridge of tergum 8 (fig. 139, M.R.8) consisting primarily of a conspicuous, short, horizontal, shallowly arched sclerotization; with anterior vertical portion represented only by a faint dorsal arm and ventral arm inapparent
rhaeba (Jordan, 1926) (p. 257)

– Mesal genitalic ridge of tergum 8 (figs 27, 32, 84, M.R.8) with a well developed vertical branch and this usually more sclerotized than horizontal fork; lacking the conspicuous arched, tanned ridge 19

19 Sternum 7 with subventral sinus not resembling a notch, even at base (figs 26, 31, 124, 7 S.), its dorsal margin sloping away from ventral at an angle exceeding more than 75° 20

– Sternum 7 with subventral sinus notch-like, at least at base (figs. 32, 40, 41, 7 S.), its dorsal margin sloping at angle less than 60° and often paralleling ventral one for at least ⅓ length of latter 21

20 Sternum 7 (figs 26, 30, 7 S.) with dorsal portion of caudal margin (at level of spiracular fossa) sloping ventrad at an angle of about 60° from vertical. Caudal margin fairly evenly rounded (not produced into a lobe) at junction with upper margin of ventral sinus. Tergum 8 (fig. 31, 8 T.) with a ventrocaudal lobe
dryadosa sp. nov. (p. 215)

– Sternum 7 (fig. 124, 7 S.) with caudal margin nearly perpendicular at level of spiracular fossa. With a caudal, short submedian lobe. Tergum 8 (fig. 117, 8 T.) lacking a ventrocaudal lobe . . . . . ***veruta*** sp. nov. (p. 252)

21 Sternum 7 with dorsal margin of subventral sinus sloping dorsocaudad from near base of sinus instead of paralleling ventral margin for ⅓ or more length of latter (figs 40, 130, 7 S.) 22

– Sternum 7 with a true subventral notch (figs 41, 49, 118, 7 S.), dorsal margin paralleling ventral for ⅓ or more of its length 23

22 Perula of bursa copulatrix (figs 40, 137, P.B.C.) with ventral ½ dilated so that ventral ⅓ twice as broad as dorsal ⅓. Paragenital morion (fig. 40, PG.M.) represented by a turned, narrow, U-shaped arc near P.B.C. Glandula vaginalis (G.VG.) single. Ventrocaudal lobe of tergum 8 (8 T.) somewhat longer than broad at base
javana (Jordan, 1933) (p. 256)

– Perula of bursa copulatrix (fig. 118, P.B.C.) elongate, scarcely broader subventrally than subdorsally. Paragenital morion near P.B.C. not tanned. Glandula vaginalis (G.VG.) preceded by an accessory "gland" (fissure) or a part of paragenital morion. Ventrocaudal lobe of 8 T. short, broad and apically blunt; its length less than breadth of base . . . . . ***loncha*** (Jordan, 1926) (p. 255)

23 Perula of bursa copulatrix vermiform (figs 78, 84, P.B.C.), not appreciably broader at middle than near ends. Paragenital morion (PG.M.) large, appearing as a broad, U-shaped loop of stout coils extending from ventral region of P.B.C. to lower portion of sternum 9 (9 S.) 24

– Perula of bursa copulatrix ovoid (figs 32, 41, 102, P.B.C.), more dilated at middle than at ends. Paragenital morion (PG.M.) reduced, not represented by a broad loop of stout coils 26

24 Upright branch of mesal genital ridge of 8 T. (figs 79, 85, M.R.8) in oblique position, and caudal fork sloping ventrocaudad at angle of 45°. Caudal margin of P.B.C. flattened . . . . . ***limi*** sp. nov. (p. 242)

– Upright branch of mesal genitalic ridge of 8 T. (fig. 78, M.R.8) subvertical and caudal fork nearly horizontal. Caudal margin of P.B.C. shallowly convex
phangi sp. nov. & subsp. nov. 25

25 Sinus above ventral lobe of sternum 7 (fig. 75, 7 S.) definitely shorter and narrower than lobe below it. 7 S. scarcely concave above submedian lobe. Paragenital morion with a tanned chord along ventral margin of inner core, near anterior margin of loop, but lacking a transverse rod-like sclerotization in the area
phangi tana subsp. nov. (p. 242)

– Sinus above ventral lobe of 7 S. (fig. 76) subequal to lobe below it. 7 S. fairly deeply concave above submedian lobe. Paragenital morion (fig. 78, PG.M.) with a transverse rod-like sclerotization near anterior margin of loop, instead of a ventral one
phangi phangi sp. nov. (p. 240)

26 Ventral, vertical fork of mesal genitalic ridge of tergum 8 (figs 32, 60, 62, M.R.8) with tanned portion as long as, or longer than, dorsal branch. Horizontal branch equally long. With a rod-like, tanned, narrow loop of paragenital morion (fig. 32, PG.M.) in line with and just caudad to base of perula of bursa copulatrix (P.B.C.) ***robinsoni*** subspp. 27

– Ventral, vertical fork of M.R. 8 (figs 41, 102) definitely shorter than dorsal branch, and horizontal branch equally short. Paragenital morion (PG.M.) lacking a rod-like, narrow loop near base of P.B.C. 30

27 Labial palpus extending beyond base of fore-trochanter. (Sarawak) ***robinsoni peregrinata*** subsp. nov. (p. 235)

– Labial palpus extending at most to apex of procoxa 28

28 Dorsal wall of vagina (figs 32, 59, VAG.) with 1–3 bead-like thickenings distad of glandula vaginalis (G.VG.) (Malayan peninsula) ***robinsoni robinsoni*** (Roths., 1905) (p. 233)

– Dorsal wall of vagina (figs 62, 64, VAG.) lacking bead-like thickenings distad of G.VG. 29

29 Ventral lobe of 7 S. (fig. 62, 7 S.) definitely longer than sinus above it[9]; with only 2 bristles on the lobe (but 1 or 2 subventrals immediately preceding it). (Java) ***robinsoni bogora*** subsp. nov. (p. 235)

– Ventral lobe of 7 S. (fig. 64, 7 S.) subequal to lobe above it; with 3 bristles on lobe. (Tioman Island) . . . . . ***robinsoni tiomanica*** subsp. nov. (p. 236)

30 With an accessory "gland" or fissure in dorsal wall of vagina, distad of glandula vaginalis (fig. 41, G.VG.). With a pair of parallel, short, tanned arcs or chords at dorsocaudal portion of duct of bursa copulatrix (D.B.C.) and another above tip of G.VG. . . . . ***angustata*** sp. nov. (p. 227)

– Lacking both an accessory "gland" distad of glandula vaginalis (fig. 102, G.VG.) and the sets of tanned chords near D.B.C. and G.VG. . ***thurmani*** sp. nov. (p. 244)

B. **Lentistivalius** gen. nov.

Diagnosis. Relatively unmodified species with: (1) Labial palpus (excluding palpiger) (fig. 140) 5-segmented. (2) First preantennal row of bristles quite or actually near frons. (3) Metatibia (figs 149, ♂; 151, ♀) with at most 2 stout dorsomarginal bristles in notches and with subdorsals unmodified and thin. (4) Movable finger (fig. 143, F.) long and narrow, with a well developed stiva (STV.). (5) Sternum 9 with distal arm (figs. 144, 145) clavate and with dilated subapical region armed with marginal spiniforms. (6) Ford's sclerite of aedeagus (fig. 148, F.SC.) with alpha-portion (figs 152, 154, ALPH.) highly developed, apically pointed and often with medial portion approximating the letter "M." (7) Crochet with body (B.CR.) and process (CR.P.) together suggesting a broad letter "U" in appearance. (8) Crochet with only narrow ventral elements linking sclerite with aedeagal pouch and hence lacking a conspicuous quasi-crochet. (9) Phylax (PHY.) slender. (10) Sclerotized inner tube (S.I.T.) of moderate length and lacking specialized armature or spurs. (11) With hood (HD.) and its deltoid flap (DEL.FL.) covering most of lateral surfaces of endchamber. (12) Female tergum 7 with lobe below antepygidial bristles (fig. 156, L.L.7) relatively short, not acuminate. (13) Spermatheca (SP. and fig. 158) at most with a very short dorsocaudal peak. (14) Mesal genital ridge of tergum 8 not

[9] Care should be taken that the ventral lobes are the same in appearance on both upper and lower sides of the specimen, for that indicates that the specimen was not distorted in mounting. If, on the other hand, one side is smaller than the other, the possible discrepancies should be considered in interpreting this couplet.

developed. (15) Tanned portions of paragenital morion somewhat reduced (fig. 160, PG.M.) rather indistinct.

Generic Description.[10] Anterior margin of head (figs 140, ♂; 141, ♀) only slightly curved below level of median sensory crater; head relatively short and high, about thrice (or somewhat more) as high (from vertex at falx to ventral margin) as long at level of uppermost bristle of row II in ♂; about 2·5–3·0 times in ♀. Ventral margin of head below eye biconvex, the 2 lobes overlapping slightly at this level. Generally with 4 rows of fairly narrow bristles and with a few "supernumerary" bristles. Labial palpus with fifth (ultimate) segment not reaching beyond procoxae. Dorsal margin of pronotum short, generally about ½ length of dorsal spines of comb (subequal to spines in *aestivalis* Jameson & Sakaguti, 1954). Mesonotum (fig. 142, MSN.) with 1 or 2 pseudosetae per side, usually subdorsal. First segment of metatarsus about 1·45 times length of second and nearly thrice length of third (which is subequal to fifth); about 2·4 times length of first segment of protarsus. Fourth vinculum (fig. 159, VC.4) usually projecting forward as a short rod. Terga 2–4 or 5 with a short subdorsal spiniform. Unmodified abdominal terga with 2 rows of bristles, preceded by a group of a few small subdorsals. Spiracular fossae of these segments broadly sagittate. Basal abdominal sternum with a few proximal submedian bristles in ♂, in ♀ with additional bristles reaching near middle of segment (fig. 159). Female with modified bristles of tergum 7 (fig. 156, U.M.B., L.M.B.) not closely resembling antepygidials (A.B.); only 1 such lower modified bristle and this not strongly displaced. Tergum 7 lacking an appreciable dorsal lobe in ♂ (fig. 147, 7 T.); in ♀, lower lobe (L.L.7) quite short, and upper one (U.L.7) particularly so.

Male. Sternum 8 (fig. 147, 8 S.) very large, nearly 1·5 times as long (near ventral margin) as high; unmodified, and lacking close-set or spiniform ventral bristles. Manubrium (figs 143, 146, MB.) broad; with ventral margin biconvex near middle. Bay of manubrium (B.MB.) extending to near apex. Immovable process of clasper (P.) with apex short and broad, subrounded or blunt. Conical process (C.P.) of clasper fairly broad, 3–5 times as tall as broad at middle. Movable finger (F.) long and thin; about 6–7 times as long (from level of apical margin of P.) as broad at middle of distal fringe (D.FR.). Stiva (STV.) long and narrow. D.FR. with about 4–5 well separated, long and relatively thin bristles; wholly or mainly on upright portion of shaft of F., proximad to curve of the stiva. Fulcral sclerite (F.S.) higher (longer) than broad; subvertical; broadest at dorsal end. Proximal arm of sternum 9 (P.A.9) in subvertical position; gradually broadening from base to near apex, where it may dilate considerably. Distal arm of sternum 9 (D.A.9) nearly length of P.A.9; widening at apical fourth to sixth, at least caudally (ventrally); with that margin bearing a subapical group of spiniforms or short, stout bristles of decreasing lengths (towards apex). Clava of D.A.9 with a lateral supramedial flap (SUP.FL.) bearing small marginal bristles, recalling *Medwayella* (but D.A.9 lacking other specialized features of *Medwayella*).

Aedeagal apodeme (fig. 148, AE.A.) resembling manubrium for most its length

[10] The genus is compared with *Medwayella* gen.nov., *q.v.*, and the differences are stressed; similarities are generally omitted.

though perhaps slightly narrower; lacking an apical appendage. Lateral laminae (L.LAM.) well sclerotized only anteriorly; ventral and caudal portions often very lightly tanned, indistinct. Aedeagal pouch well tanned ventrally (fig. 152, AE.P.-V.), but less so laterally (AE.P.-L.); unsclerotized at base and girdle hence not clearly demarcated; lacking obvious sclerotized connections with crochet process (CR.P.) except for a tail-like ventral process at the base of CR.P. and narrow ventral elements (*cf.* fig. 153, ventral aspect) and therefore lacking a quasi-crochet (*cf.* figs 22, 23, Q.C.). Hood (HD.) without notch or sinus, although at times (fig. 155) concave ventrally; covering most of endchamber; its deltoid flap (DEL.FL.) not produced dorsally into an apical acuminate process. Anterior margin of DEL.FL. well caudad of fulcrum (AE.F.); caudodorsal origin near cephalodorsal angle of Ford's sclerite (F.SC.) rather than upper margin of body of crochet (B.CR.). Lateral lobes (L.L.) greatly reduced; inapparent. Sclerotized inner tube (S.I.T.) sub-horizontal; about 4–6 times as long as broad at middle; lacking dorsal or ventral spurs or other specialized armature. Ford's sclerite (F.SC.) very large and constituting dominant sclerite in endchamber, and with alpha (ALPH.) and securifer (SEC.) components fused and distinctions apparent only at margins (*cf.* fig. 153, ventral aspect). ALPH. a major component of F.SC., and its dorsal, ventral and apical margins with characteristic shapes in various species. Securifer (SEC.) comparatively reduced (in lateral aspect); often produced into an apical spur. Phylax (PHY.) fairly long and narrow, somewhat crescentic in shape, extending from near base of CR.P. to near ventral margin of F.SC. and apex of pivotal ridge (PIV.R.), which is lightly tanned. Pivotal chord (PIV.CD.) weakly sclerotized. Crochet boomerang-shaped or broadly U-shaped; body of crochet (B.CR.) subvertical and crochet process (CR.P.) sub-horizontal. Aedeagal fulcrum (AE.F.) quite narrow. Crescent sclerite (C.S.) moderately long; satellite sclerite (SAT.S.) relatively so; latter overlying base of S.I.T., i.e., appearing as if "within" it. Vesicle (V.) lightly tanned. Third apodemal rod (AP.R.) of endophallus not particularly well developed. Caverna spiculosa (CAV.SPIC.) long, commencing subdorsally but at about level of base of fulcrum.

Female. Spermatheca (figs 156, SP. and 158, 161) longer than broad; bulga (B.) with internal striae; lacking a truly distinct peak; but at times with a short dorsocaudal bulge. Hilla (H.) with an apical papilla (PAP.); base inserted fairly deeply into bulga, protruding element therefore appearing relatively broad in relation to length; internal portion with striae. Duct of spermatheca (D.SP.) bearing internal sclerotized rings at least near dilated portion (DIL.P.). Dorsal region of perula of bursa copulatrix (P.B.C.) associated with 2 sclerotized rod-like or dot-like bodies. Duct of bursa copulatrix (D.B.C.) lightly tanned. Paragenital morion (fig. 160, PG.M.) somewhat reduced; inconspicuous and rather ventral in position, near apical region of bursa copulatrix. Sternum 7 (figs 156, 160, 7 S.) with a subventral sinus. Ventral anal lobe (V.A.L. and fig. 157) with base short; apical margin fairly long, somewhat sinuate; with a gap between submesal and subapical groups of bristles. Anal stylet (A.S.) fairly long and narrow and lacking long subapical bristles. Tergum 8 (8 T.) lacking a conspicuous lobe at ventrocaudal corner. Mesal genitalic ridge of tergum 8 undeveloped. Spiracular fossa 8 (8 SPC.) medium-sized; upright portion ovate. Sternum 8 (8 S.) flask-shaped and with short apical bristles.

The type of the genus is *L. vomerus* sp.nov., described below. Here also belong the "*Stivalius ferinus*-group" of Smit (1958), viz., *ferinus* (Rothschild, 1908), a parasite of shrews on the Indian subcontinent, Ceylon and South China; *insolli* (Traub, 1950), a flea of birds in the mountains of Malaya; *aestivalis* (Jameson & Sakaguti, 1954) infesting *Apodemus speciosus*, a wood-mouse in Japan; and *alienus* (Smit, 1958) stated by the author to be a parasite of rodents, and occurring in East and Central Africa.

COMMENT. The generic name is derived from the Latin term *lentes*, meaning *flexible*, and refers to the remarkable facility of this genus to adapt to a broad variety of hosts, in widely separated areas, as indicated above. This point is discussed further below in the second article in the series, dealing with convergent evolution, and in the third, which concerns zoogeography.

1. **Lentistivalius vomerus** sp. nov.

TYPE MATERIAL. Holotype ♂, allotype ♀ (B-19249) ex *Tupaia montana*; NORTH BORNEO (EAST MALAYSIA, Sabah): Mt. Kinabalu, Tenompak; elev. 4500 ft; 16.VIII.1953; Coll. R. Traub for U.S. Army Medical Research Unit (Malaya). Paratypes, all from North Borneo (East Malaysia, Sabah) as follows:

♂	♀	Host	Locality, Date and Collector	
99	75	*Tupaia montana*	Mt. Kinabalu, vicinity of Tenompak; elev. 4500–5500 ft; July 1, 1951	R. Traub
			August, 1953	R. Traub
			May, 1952	J. R. Audy
			Feb.–Mar. 1964	Lord Medway & Cambridge Univ. Exped.
			Dec. 1965	Lim Boo Liat & D. Heyneman for G. W. Hooper Foundation
3	1	,, ,,	Mt. Kinabalu, vicinity of Mari Parei; elev. 4000–5100 ft; 24–25.VIII.53	R.T.
1	–	,, ,,	Mt. Kinabalu, Lumu Lumu; elev. 6300 ft 23.VII.1951	R.T.
–	3	,, ,,	Mt. Kinabalu, Kamborangah; elev. 7200 ft 3.VI.1952	J.R.A.
6	4	,, ,,	Mt. Trus Madi, Pampang, Ulu Kaingaran; elev. 4000 ft 19.VII–7.VIII.53	J.R.A.
1	–	,, ,,	Mt. Trus Madi; elev. 7500 ft 30.VIII.1956	Cambridge U. Exped.
5	3	*Dendrogale melanura*	Mt. Kinabalu, Lumu Lumu; elev. 6300 ft 21.VII.1951	R.T.
–	1	,, ,,	Mt. Kinabalu, Mari Parei; elev. 5100 ft 25.VIII.1953	R.T.
–	1	,, ,,	Mt. Kinabalu, Tenompak; elev. 4500 ft 30.VIII.53	R.T.

♂	♀	Host	Locality, Date and Collector (continued)	
3	–	,, ,,	Mt. Trus Madi, Pampang, Ulu Kaingaran; elev. 4000 ft 1.VIII.1953	J.R.A.
–	1	,, ,,	Mt. Trus Madi, Kidokarok; elev. 5000 ft 3.IX.1956	Cambridge U. Exped.
2	1	*Dremomys everetti*	Mt. Kinabalu, Tenompak; elev. 4500 ft 16.VII.51, 31.VIII.53	R.T.
1	1	,, ,,	Mt. Kinabalu, Tenompak; elev. 9800 ft Dec. 1965	L.B.L.
1	1	,, ,,	Mt. Kinabalu, Lumu Lumu; elev. 6300 ft	R.T.
2	1	,, ,,	Mt. Trus Madi Aug.–Sept. 56	Cambridge U. Exped.
1	1	,, ,,	Mt. Trus Madi, Pampang, Ulu Kaingaran; elev. 4000 ft July-Aug. 53	J.R.A.
–	3	*Hylomys suillus*	Mt. Kinabalu, Tenompak; elev. 4500–5000 ft 16.VII.59, 12–20.VIII.53	R.T.
1	–	,, ,,	Mt. Kinabalu, Mari Parei; elev. 5100 ft 25.VIII.53	R.T.
3	–	*Rattus alticola*	Mt. Kinabalu, Tenompak; elev. 5500 ft 16.VII.1951	R.T.
–	1	,, ,,	Mt. Kinabalu, Mesilau Base Camp 10.II.1964	L.M.
–	1	*Rattus whiteheadi*	Mt. Kinabalu, Tenompak; elev. 5500 ft 19.VII.1951	R.T.
2	2	*Rattus* sp.	Mt. Kinabalu, Bundu Tuhan; elev. 4000 ft 26.V.1952	J.R.A.
1	1	,, ,,	Mt. Kinabalu, Kamborangah; elev. 7200 ft 5.VI.1952	J.R.A.
–	1	*Haematortyx sanguiniceps*	Mt. Trus Madi, Pampang, Ulu Kaingaran; elev. 4000 ft 22.VII.1953	J.R.A.
1	–	Shrike	Mt. Kinabalu, Lumu Lumu, elev. 6300 ft. 23.VIII.1951	R.T.

Holotype (U.S.N.M. number 71609), allotype and five pairs of paratypes deposited in U.S. National Museum. Remaining paratypes distributed as for *M. dryadosa.*

Diagnosis. Close to *L. insolli* (Traub, 1950) (new combination) and even agrees with it in that the dorsal and submedian tanned margins of the alpha-portion of Ford's sclerite (figs 152, 154, ALPH.) are shaped somewhat like the letter "M." Instantly separable in that the new species lacks modifications of the pronotal comb of *L. insolli* which have been cited (Traub, 1969) as being characteristic of bird-fleas, viz.: (1) A large number (about 28 in *L. insolli*) of narrow, quite straight, mainly horizontal, parallel spines in a comb which does not descend over third vinculum. (2) Axis of the bases of the majority of spines in comb slopes anteroventrad. Instead, in the new species, there are only about 20 spines in the pronotal comb (fig 140) and the spines are broader, i.e., no significant gaps between them and yet height of comb is the same—extending to a level just above VC.3; middle 6 spines fairly concave, and axis of the bases of the main spines largely subvertical, not oblique. It has been pointed out (Traub, 1966) that in bird-fleas (and presumably other ectoparasitic

insects parasitizing birds) the bristles of the body are longer and thinner than in relatives infesting mammals, and this is also true for *L. insolli* versus *L. vomerus*, e.g., caudoventral bristle of mesepimere 31 times as long as broad at base in the former species and only 23 times in the latter (fig. 142, MPM.).

Further separable from *L. insolli* as follows: (1) movable finger (fig. 143, F.) proportionately much broader in new species, i.e., only 4·4 times as long (from apex of P.) as broad immediately below stiva (STV.), instead of more than 7·6 times (fig. 146). (2) Distal arm of ♂ sternum 9 (D.A.9 and fig. 144) with apical margin ovate, not oblate (fig. 145); margin above subapical spur curved and slanting, not straight. (3) Spermatheca relatively longer and narrower, i.e., about 2·2 times as long as broad at maximum diameters (figs 158, 160) when undistorted, instead of 1·7 times.

Near *L. aestivalis* but instantly separable as follows: (1) Deltoid flap (fig 152, DEL.FL.) virtually squarely meeting ventral margin of hood (HD.) at anteroventral corner instead of being produced into a long, acuminate, curved structure (fig. 155). (2) Crochet process (CR.P.) narrowly ovate, nearly 5 times as long (to middle of base B.CR.) as broad at middle, instead of being trapezoidal and broader, viz., 2·5 times as long as broad. (3) Lobe above subventral sinus of ♀ sternum 7 (fig. 156, 7 S.) at most with a shallow sinus instead of one that virtually equals that below it, so that this region is practically evenly biconcave. Differences from other species of *Lentistivalius* are indicated in the key which follows the description below.

Descriptive notes.[11] Head (figs 140, ♂; 141, ♀). With preantennal portion of head of ♂ about 2·4 times as high as long at level of eye-bristle and slightly more than thrice as high as long at level of uppermost bristle of row II; in ♀ comparable figures are 2·3 and 3. With preantennal bristles in 4 rows except for a fair-sized supernumerary between rows II and III. Labial palpus with apical segment 1·7 times length of penultimate (fourth); extending to about apex of procoxa.

Thorax. Pronotum (fig. 140) narrow; dorsally with spines of comb about 2·5 times length of notum; with 2 rows of bristles, but first row highly abbreviated. Pronotal comb with a total of about 20 spines, of which, in ♂, numbers 2 – 8 per side (counting dorsalmost as number 1) are slightly convex, narrowing gradually from base to apex; bluntly pointed or subovate at apex; bases of middle spines inclined ventrocaudad at an angle of about 20°; spine number 7 the broadest, but only slightly exceeding its mates, about 5 times as long as broad at middle. Mesonotum (fig. 142, MSN.) with 4 rows of bristles; first row abbreviated; those of first 2 rows short; with 1 subdorsal pseudoseta per side. Mesepisternum (MPS.) with oblique row of 4 bristles; dorsalmost (first) of these near middle of caudal margin; slope anteroventrad; first and third bristles long; lowest subventral in position. Mesepimere (MPM.) with 2 rows of 3 long bristles; that near ventrocaudal angle longest. Third vinculum (VC.3) with dorsal margin basally quite flat, distal ½ concave; axis about 35°–45° from horizontal. Lateral metanotal area (L.M.) with external measurements slightly longer dorsally than high, but internal, relatively untanned region somewhat higher than long. Metepimere (MTM.) with 3 rows of 3–4 bristles each and those of last

[11] The species is compared with *M. dryadosa*, *q.v.*, and the differences are stressed; similarities are generally omitted.

row with intercalaries (usually 2 such between ventral pair of long ones); caudal margin becoming shallowly convex near level of spiracular fossa.

Legs. Metacoxa with a group of about 14–16 short, thin, mesal bristles on apical $\frac{1}{3}$, anterior to internal rod. With 5–8 submedian lateral bristles in 2 irregular longitudinal rows of profemur. Meso- and metafemora with 4–5 small subdorsal bristles on apical $\frac{1}{2}$; 3 ventromarginals on distal $\frac{1}{5}$ and 2 submedians near spiniform member of apical pair of stout bristles. Protibia in ♂ with first (apical) and fifth members of dorsomarginal pair of bristles much shorter and somewhat longer than their mates, hence appearing as "single" bristles, in ♀, with 3 such single bristles between third and fifth pairs, and since first pair is similarly modified, this sex here bears an incipient comb of false spines. Other legs with dorsomarginals paired in usual manner (metatibia, figs 149, ♂; 151, ♀), and only D.M.4 single; ♂ with 3 non-marginal rows of lateral bristles and only 1–2 supernumerary bristles; ♀ with 4 such rows. An apical bristle of mesotarsus I–III and of metatarsus II and III, reaching to middle of succeeding segment. Proportions of tarsi essentially as that cited for *L. insolli* (Traub, 1950). Metatarsus with apical segment with 6 pairs of lateral plantar bristles, but third displaced towards midline (fig. 150).

Abdomen. Basal sternum of ♀ with group of about 7–10 small, thin, lateral bristles commencing near vinculum and extending to about anterior $\frac{1}{3}$ and ventral $\frac{1}{3}$; in ♂ with at least the bases for about 6 such hair-like bristles, but group nearer to anterodorsal region. Terga 2–5 usually with 1 subdorsal apical spinelet. Spiracular fossae in unmodified terga of ♂ symmetrical and narrowly sagittate (e.g., fig. 147, 7 SPC.); in ♀ shorter and broader and dorsal margin more convex than ventral (fig. 156, 7 SPC.). Representative sterna of ♂ with ventral group of 3 long bristles preceded by a group of 3 smaller ones and 1 more anterior ventromarginal one (e.g., 7 S.). In ♀ (fig. 156, 6 S.) such sterna with 4 bristles in caudal row, but, except for 6 S., uppermost usually small; middle subventral group of 4–6 small ones; anteriormost, 3 or 4. Uppermost antepygidial bristle (A.B.) in each sex somewhat less than half of lower one. Female with only 2 adjacent bristles modified so as to suggest A.B., and only somewhat so, viz., dorsomarginal one (U.M.B.) rather dark and stout, but not displaced; lower one (L.M.B.) fairly close to A.B. but not as long, dark and stout as upper A.B. Dorsal lobe of tergum 7 (U.L.7) not produced caudad above and between bases of A.B.; margin below A.B. (L.L.7) scarcely extending beyond A.B., viz., not truly lobate.

Modified Abdominal Segments—Male. Tergum 8 (fig. 147, 8 T.) slightly more than twice as high as long at middle; somewhat dilated ventrally; not extending below level of base of ventral anal lobe (V.A.L.). Vertical arm of spiracular fossa 8 (8 SPC.) rather more than thrice as high as broad at middle; dilated horizontal section only 1·25 times longer than high or than vertical arm is broad at middle. Sternum 8 (8 S.) nearly twice as long (along ventral border) as high at middle (level of first dorsal bristle); ventral margin sloping towards middle much more than upper, but quite straight for most its length; cephalic margin shallowly concave; caudal margin quite straight. 8 S. with bristles approximately as follows: a dorsomarginal row of 4, commencing just beyond midpoint, where margin starts to curve caudoventrad, and terminating at caudal $\frac{1}{6}$, the last bristle by far the longest; with 5 subdorsal bristles,

arranged 3–2, the first ventral row near midline, the second row oblique and in line with first of dorsomarginals; a horizontal row of 3 along midline, starting at anterior $\frac{1}{3}$ and terminating near margin; another horizontal row of 3 just below this, but bases somewhat more cephalad and otherwise symmetrical; a group of 2 subventrals, submedian, in a horizontal row; with 8–10 ventromarginals, or contiguous short bristles, arranged in twos and threes, starting near midline and terminating subcaudally; none of the above bristles anterior to cephalic $\frac{1}{4}$, and most caudal of midline. Immovable process of clasper (fig. 143, P.) dorsally very broadly and shallowly rounded; with a short dorsomarginal bristle near middle of dorsal margin and another, longer, subapical one near apex of P.; caudal margin very shallowly sinuate distad of marked sinus at base of manubrium (MB.). Conical process (C.P.) about 3·5–4 times as long a broad at middle; caudal margin straight. Movable finger (F.) with portion distad of apex of P. about 5·4 times as broad at level just proximad of curve of stiva (STV.) (*cf.* fig. 1, j–k) and 3·7 times as broad at level of apex of C.P.; the difference representing the degree of gradual narrowing of F. from base towards apex. F. with anterior and posterior margins otherwise appearing parallel; anterior margin somewhat convex but becoming slightly concave between proximal and third sensilla of group of 4 (S.G.). Stiva (STV.) fairly long and quite narrow; length (*cf.* fig. 1, measured from k–o to p) about 1·3 times subapical width of F.(j–k) and about $\frac{9}{15}$ of total length of apex of F. (l–p); about thrice breadth of middle of stiva. Distal fringe (D.FR.) of 4 widely spaced, relatively thin, long bristles, commencing at level of middle of F. (above P.) and terminating at level of middle of STV. Fulcral sclerite (F.S.) essentially a right triangle with base and hypotenuse slightly sinuate and with altitude concave and apex blunt; length about 1·7 times breadth at dorsal margin, thrice that at middle and about 7 times that at apex. Manubrium (MB.) fairly broad; length (as measured from base of dorsal margin, where base of F. angles ventrad) about 1·9 times breadth of MB. at anterior ventral bulge; dorsal margin slightly convex to near apex, where it becomes sinuate and fairly straight subapically; ventral margin parallel to dorsal near apex, somewhat sinuate to anterior bulge and here biconvex but sinus between bulges short; caudal bulge longer than anterior; apex slightly upturned; anterior margin, at tip, relatively straight. Tergal apodeme of ninth segment (T.AP.9) relatively narrow; length (to base of F.) nearly 6 times breadth at middle. Proximal arm of sternum 9 (P.A.9) about 6·5 times as long (*cf.* fig. 1, from aa–bb to level of ii) as broad at base (gg–hh); length thrice breadth at bulge of anterior margin at distal $\frac{1}{3}$ (dd); 2·2 times breadth at apex (aa–bb). P.A.9 with dorsal (posterior) margin slightly biconcave; anterior margin fairly concave at distal $\frac{1}{3}$ (aa–dd) and thereafter quite straight; dorsal margin shallowly sinuate except at corners. Distal arm of sternum 9 (D.A.9 and fig. 144) nearly 6 times as long (ii–qq) as broad at middle; margins sinuate but parallel to above apical $\frac{1}{3}$, where caudal margin becomes oblately convex, so that distal portion resembles the head of a mace with posterior and apical margins oblate. Armature of mace-head consisting of marginal spiniforms, as follows: a stout sub-proximal one, above which are 4–5 smaller, paler spiniforms, commencing at middle of distal margin, and below which is 1 fairly long spiniform with a longish subspiniform at base of dilated portion. D.A.9 with a subapical nubbin or short, stout, spur on anterior margin, above a short notch

with well tanned margins. Dilated or club-like apex of D.A.9 about 1·4 times as long (from basal subspiniform) as broad at level immediately below subapical notch.

Aedeagus—Lateral Aspect (figs 148, 152, 172). Aedeagal apodeme (fig. 148, AE.A.) with middle lamina (M.LAM.) more tanned than lateral plates (L.LAM.); latter only well sclerotized near anterior end, and ventral and caudal portions semimembranous, indiscrete, with ventral region appearing confused with penis rods. M.LAM. about 4·4 times as long (from anterior edge of crescent sclerite, (C.S.), at base of aedeagal fulcrum, (AE.F.)) as broad at anterior margin of bay of middle lamina (B.M.L.). AE.A. significantly narrowing only at level of anterior edge of B.M.L.; rather resembling MB. in shape but not as broad; apex somewhat upturned. B.M.L. extending to apical ¼. Median dorsal lobe (M.D.L.) sloping dorsocaudad at angle of about 45° commencing at level of AE.F.; straight to even, broad curve at level of Ford's sclerite (F.SC.). Aedeagal pouch (AE.P.) with base very lightly tanned and hence not representing a typical girdle, but with usual elements proceeding dorsad to top of apodeme, near anterior end, and en route blending with extensions of L.LAM. which project ventrad towards fulcrum and which join indistinct ventral margins of L.LAM. from anterior end of apodeme. Ventral wall of pouch (fig. 152, AE.P.-V.) well tanned. Hood (HD.) covering endchamber as a symmetrical cowl whose ventral margin is fairly straight and extends from tip of apices of Ford's sclerite (F.SC.) to apex of crochet process (CR.P.); extended dorsad as the deltoid flap (DEL.FL.) and terminating acutely in subdorsal region at level of basal ¼ of sclerotized inner tube (S.I.T.); dorsal and ventral margins in the main at right angles to cephalic margin. Ford's sclerite (F.SC.) largest (in mass) of sclerites in endchamber; shaped like a broad, low arch with longitudinal axis horizontal. Most conspicuous part of alpha-portion (ALPH.) an M-shaped ridge or thickening whose one leg is long, subdorsal and subhorizontal; opposite leg only about half as long and with cross-bar in the form of a shallow "V", and apical. Distad of the "M," with a bell-shaped dome which is longer than high and terminates apically in an eccentric (ventral) short stalk, contiguous with a caudal acuminate process of the securifer (SEC.) so that tip of F.SC. is bifid. Securifer semi-circular, its lower (anterior) leg a short, fairly blunt lobe. Pivotal ridge (PIV.R.) lightly sclerotized and its chord (PIV.CD.) short, narrow and straight. Sclerotized inner tube (S.I.T.) nearly 7 times as long (from caudal apex of Y-sclerite (Y.S.) to middle of apex) as broad at level of caudal margin of crochet process (CR.P.) and 3·3 times as broad at sub-basal thickening (i.e., at short ventral bulge); axis very slightly arched to short up-curve at apex, where dorsal margin bears a short peak. Crescent sclerite (C.S.) fairly long and narrow; borders at times indiscrete because of unusual degree of tanning of lateral shafts of capsule (L.S.C.) and proximity of relatively large satellite sclerite (SAT.S.). Caudal extremity of C.S., and all of SAT.S., overlying base of S.I.T. Central sclerite (CEN.S.) closely appressed to fulcral medial lobe (FUL.M.L.); the two together appearing as the upper part of an arrowhead. Y-sclerite (Y.S.) conspicuous as a large, sub-triangular sclerite as broad as base of fulcrum and ventral to it, and with a narrow, rod-like fork extending dorsocaudad to above mid-line of S.I.T. at level of apex of C.S. Dorsal virga (D.V.) indistinct. Phylax (PHY.) a crescent whose chord is about 8 times its breadth at middle; lying across middle of S.I.T. so that upper ½ is above S.I.T., with apex near

ventral tip (base) of F.SC.; lower ¼ of PHY. below S.I.T. and contiguous with crochet. Body of crochet (B.CR.) terminating at base of F.SC.; clavate, broadest subapically; ventral portion about ½ as broad as upper, as sclerite curves caudad. Crochet process (CR.P.) digitoid, directed caudad and proceeding slightly beyond level of apex of B.CR. With a short spur pointing cephalad and arising from anteroventral angle of crochet and merging with ventral walls of aedeagal pouch. Upper member of penis rods (P.R.) extending to near apex of apodeme; lower members shorter; both paralleling ventral margin of L.LAM. Ventral virga (V.V.) stout; sclerotized to level of about base of AE.P. Third apodemal rod (AP.R.) well tanned to base of AE.P., but apparent for most its length, which equals P.R.

Aedeagus—Ventral Aspect (fig. 153). Hood (HD.) bifid apically. Ford's sclerite with distal ½ consisting of broad, sub-quadrate, right and left components fused near base, at midline, but well separated distad; alpha (ALPH.) and securifer (SEC.) elements forming blended and integral parts of each ½ (and hence here constituting merely topographic terms useful in taxonomic distinctions). Basal ½ of F.SC. semicircular. Deltoid flap (DEL.FL.) covering lateral ⅛ of ventral surface. Phylax (PHY.) with ventral portion of each straddling sclerotized inner tube (S.I.T.) and sloping towards midline dorsally so that apices are virtually contiguous, above S.I.T. and here connected by a membrane; dorsal region stouter (from lateral surface towards mesal) than ventral. Wall of aedeagal pouch with ventral extensions (P.W.EX.) leading to floor of base of CR.P. Lateral lobes so ventral in position they appear like mesal structures. S.I.T. dilated subapically. Satellite sclerite (SAT.S.) along midline; well distad of base of S.I.T. and mesad of apices of crescent sclerites (C.S.). Lateral shafts of capsule (L.S.C.) relatively broad as well as long. Vesicle (V.) broad. Y-sclerite with ventral components broadly triangular with winged angles at base, serving as floor of capsule; more dorsal fork with symmetrical, broad, ovoid projections extending more mesad. Fulcral lateroventral lobes (FUL.L.L.) short, fairly widely separated. Caverna spiculosa (CAV.SPIC.) very long, somewhat fusiform, and occupying much of breadth of apodeme.

Female. Sternum 7 (fig. 156, 7 S.) about 1·5 times as high as long at maximum diameter (i.e., level of maximum curvature of median lobe on caudal margin); anterior margin very shallowly convex; dorsal margin oblate; caudal margin with a subventral short sinus which is scarcely more than ⅓ of height of lobe beneath it. 7 S. with lobe above this sinus somewhat concave (at times more so than in figure) but soon straightening and sloping antero-dorsad from level of apex of ventral anal lobe (V.A.L.); margin rather concave from level of dorsal part of sensilium (SN.) to upper part of spiracular fossa 8 (8 SPC.). 7 S. with vertical caudal row of 4 long bristles, of which 1 is ventral and 1 subventral, about at level of middle of ventral lobe; 1 slightly above level of sinus and uppermost above third by distance equal to mouth of sinus; this row removed from caudal margin by distance equivalent to ½ length of lowest bristle. This row preceded by a vertical group of about 10 smaller bristles, most of which are in a line but some subventrals displaced caudad, as is a fairly long ventromarginal. Latter group preceded by about 10 bristles in 2 short, irregular, subventral rows of 3–4 and 4–5, plus 1 or 2 marginals or submedians out of line. Tergum 8 (8 T.) with caudal margin straight and oblique to short lobe at

ventrocaudal angle; with 2 rows of small bristles, usually 2–5, immediately before vertical portion of 8 SPC.; with a subventral, horizontal row of 3 fairly long bristles, preceded by 1 small one and with the caudalmost inserted before apex of sternum 8 (8 S.); with an oblique subvertical row of 3 bristles at level of base of V.A.L., of which uppermost is at level of upper member of ventral genital pair at caudal margin and lowest in line with ventrocaudal lobe; with 2 vertical rows of more anterior bristles; the first (anteriormost) of 3 small ones in line with ventral base of 8 S. and lowest of which was cited above as preceding subventral horizontal row; the second, of 3 small submedians, of which ventralmost is in line with first member of subventral horizontal row; third row of 4 submedians in line with second large member of subventral horizontal row. 8 SPC. with vertical portion broadly ovate, about twice as high (including section overlapped by horizontal arm) as long at middle; horizontal portion with tanned area about 2·2 times as long as broad at base. Dorsal anal lobe (D.A.L.) with a dorsomarginal row of 3 or 4 bristles; and 1–2 tiny ones contiguous with base of sensilium (SN.); caudalmost dorsomarginal very long; with a subdorsal row of 3, of which caudalmost is long, in line with last dorsomarginal and above base of anal stylet (A.S.); with a pair of subventrals immediately preceding long bristle ventrad to base of A.S.; with 2–3 small, scattered submedians. A.S. about 4 times as long as broad at middle; with a very small subapical bristle dorsal and ventral to base of apical long bristle. Ventral anal lobe (V.A.L.) angulate, with anterior margin less than $\frac{3}{8}$ length of ventral margin; with 3 groups of ventromarginal bristles—a subequal but longish pair at anteroventral angle (at times represented by a single bristle); a long one at anterior fourth (at times paired here, e.g., when first is single), and a long pair on a short mesal flap at caudal third or fourth. Spermatheca with outlines variable, depending upon position in slide-preparation. Typically (fig. 156, SP. and fig. 158), as when seen in lateral aspect, with bulga elnogate-oval, approximately twice (or 2·2 times) as long (maximum diameter) as broad in middle. Atypical appearance shown in figs 160 and 161, and latter particularly misleading, for bulga seems only 1·7 times as long as broad. Bulga typically with ventral margin fairly flat except for anterior up-curve at level of apex of lower margin of internal portion of hilla (H.); dorsal margin anteriorly quite straight but with a subtruncate, short posterior bulge; caudal margin convex. Hilla (H.) inserted into lumen of bulga for about $\frac{1}{2}$ its length; external portion recurved at middle and apex rather flat, oblique below the apical papilla (PAP.); internal portion longer than breadth (inner measurements) at middle; of fairly uniform breadth to near apex. Bursa copulatrix with a pair of characteristic tanned, short rods or ill-defined thickenings flanking apex of perula (P.B.C.), one anterior and one posterior, at base of sac of bursa (SAC.). P.B.C. narrow, unmodified, scarcely differentiated from duct (D.B.C.) below it. Dilated portion of bursa (DIL.P.) weakly tanned and subequal in length to dorsal part of SAC. Duct of spermatheca with internal striae usually visible near entrance into SP. and near DIL.P. Paragenital morion (PG.M.) reduced to an indefinite semimembranous area near upper wall of vagina (VAG.) at genital orifice and overlying ventral portion of bursa; with elements lying anterior to latter. Glandula vaginalis (G.VG.) short, broad and indistinct, partially underlying expanded base of apical wall of bursa. Duplicatura vaginalis (D.VG.) indiscrete, at base of

vertical portion of SAC., which broadens at level of vagina, anterior to orifice of bursa copulatrix.

Host–relationships and Distribution and other comments. The name *vomerus* is derived from the Latin word for plough-share and was selected not only because the shape of the movable finger resembles a plough-handle, but because Ford's sclerite, as seen in dorsal or ventral aspect, suggests the share of the plough, with the elongate crochet-processes serving as handles, while, in lateral aspect, the crochet-processes themselves suggest the share as seen from the side.

Lentistivalius vomerus sp. nov. is obviously common in the mountains of North Borneo, especially at elevations of about 4000–6300 ft, where it parasitizes primarily *Tupaia montana* but apparently also infests other small mammals in the same habitat, e.g., *Dendrogale* (a tupaiad), ground-squirrels and rats, on or near the forest-floor. It was collected on occasion at higher elevations, even above 9000 ft. The absence of records from tree-squirrels on Mt. Kinabalu and Mt. Trus Madi is significant, since I examined at least 50 such *Callosciurus* in the former area, and Lim Boo Liat, M. Nadchatram, J. R. Audy and others of our colleagues also collected fleas from tree-squirrels in both regions.

Illustrations

140. Head and prothorax (♂)
141. Head (♀)
142. Meso- and metathorax (♂)
143. Clasper and segment 9
144. Distal arm of sternum 9
147. Modified abdominal segments (♂)
148. Aedeagus
149. Metatibia (♂)
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151. Metatibia (♀)
152. Apical region of aedeagus (lateral)
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156. Modified abdominal segments (♀)
157. Anal lobes and stylet (♀)
158. Spermatheca
159. Abdominal segments 2 (♀)
160. Spermatheca and genitalia
161. Spermatheca (variation)
172. Apical region of aedeagus

2. Key to the known species of **LENTISTIVALIUS** gen. nov.

1 Pronotal comb with a total of about 26–28 spines, close-set, their bases contiguous; spines narrow, about 6·5 times as long as broad at middle; most of spines parallel and similar in shape. (Malayan bird-fleas)[12] . . . . . ***insolli*** (Traub, 1950)

– Pronotal comb (fig. 140) with about 18–20 spines; spines distinctly separated at bases; generally broad—about 5·4 times (or less) as long as broad at middle (narrow in *L. ferinus*, but not close-set); spines variable in shape and inclination, at least regarding dorsal versus ventral ones. (From mammals; in other areas) 2

2 First preantennal row of bristles spiniform in shape. With 4–5 spiniforms bordering frontal margin of head. Pronotal comb[13] with spines mainly concave dorsally and with apices broad and rounded. (On shrews; Indian subcontinent and southern China) . . . . . ***ferinus*** (Rothschild, 1908)

– First preantennal row of bristles unmodified; only ventral 2 bristles bordering frontal margin (fig. 140). Pronotal comb with spines fairly straight, apices narrowed, pointed (fig. 140) or angled.[14] (Generally on tupaiads or rodents; Africa or Asiatic-Pacific islands) 3

[12] See next article in series for illustrations of pronotal combs of other *Lentistivalius*, viz., fig. 18 for *insolli*.
[13] See fig. 15 in next paper.
[14] See fig. 16 in next paper.

3 With only 1 row of bristles on pronotum. Distal arm of ♂ sternum 9 lacking a subapical spur on anterior margin. ♀ sternum 7 with subventral sinus near middle of lower ½ of caudal margin. ♀ spiracular fossa 8 with vertical portion relatively broad, viz., less than twice as long as broad at middle. (Africa) . ***alienus*** (Smit, 1958)

– With 2 rows of bristles on pronotum (fig. 140). Distal arm of ♂ sternum 9 with an anterior subapical spur (figs 144, 145). ♀ sternum 7 with subventral sinus much closer to ventral margin than to middle of caudal margin (fig. 156, 7 S.). ♀ spiracular fossa 8 with vertical portion more than twice as long as broad at middle. (Borneo and Japan) 4

4 Deltoid flap of aedeagus with a ventrocaudad-directed acuminate process arising at anteroventral corner (fig. 155, DEL.FL.). Crochet-process (CR.P.) only about 2·5 times as long as broad at middle. ♀ sternum 7 definitely biconcave, upper sinus on caudal ½ taller than and nearly as deep as subventral one. (Japan) ***aestivalis*** (Jameson & Sakaguti, 1954)

– Deltoid flap of aedeagus relatively squared at anteroventral corner, lacking an acuminate projection (fig. 152, DEL.FL.). Crochet-process (CR.P.) nearly 5 times as long as broad at middle. ♀ sternum 7 with only one distinct sinus, and that subventral (fig. 156, 7 S.). (N. Borneo) . . . . ***vomerus*** sp. nov. (p. 272)

C. ***Stivalius*** Jordan & Rothschild, 1922, *Sensu Strictu*

Stivalius Jordan & Rothschild, 1922. Ectoparasites 1 : 249–250. Type of genus: *S. ahalae* (Rothschild, 1904).
Stivalius, Holland, 1969, Mem. ent. Soc. Canad. No. 61 : 14.

A major contribution to our understanding of *Stivalius s. lat.* was made by Holland (1969) when he created seven new genera based upon New Guinean species and described and illustrated new species in these taxa. In this connection, Holland aptly and capably defined *Stivalius s. str.*, thereby presenting a standard by which his new genera could be compared, and easing the work of those who followed him. In order to facilitate evaluation and characterization of the new genera described above in the present opus, *Stivalius* Jordan & Rothschild *s. str.* is now redescribed, citing aedeagal and some other characters not previously mentioned, so that direct comparison with the new genera in the present paper is feasible. A new subspecies of *S. cognatus* Jordan & Rothschild, 1922, is described to illustrate the typical features of the taxon.

Diagnosis. Instantly separable from related taxa by: (1) the elongated sclerotized inner tube (figs 170, 173, 174, S.I.T.) which is 9–30 times as long as broad at middle and arched at least for apical ½, and (2) the bursa copulatrix, which appears either grossly swollen throughout and coiled for most its length (fig. 176, B.C.) or else the apical ½ is folded upon itself (fig. 162) (*S. phoberus* Jordan & Rothschild, 1922). Also characteristic as follows: Movable finger (fig. 165, F.) long and narrowed with well developed stiva (STV.). Conical process (C.P.) broad. Ford's sclerite (figs 170, 173–174, F.SC.) large—longer than adjacent sclerites, narrowed subapically and terminating in 1 or 2 hook-like projections. (This fact, and elongated S.I.T., probably account for the noteworthy absence of ventral paramere-like processes, e.g., the crochet lacks a caudad-directed arm.) S.I.T. bearing a distinctive basal sclerite (L.W.AR.). Distal arm of sternum 9 (figs 167–169, D.A.9) apically with a short lobe (A.LB.9) bearing bristles, and a mesal apicocaudal flap or expansion (AC.F.9) bearing

marginal subspiniforms. Labial palpus 5-segmented (excluding palpiger). Tibiae with some stout subdorsal setae next to, or incorporated within, dorsomarginals so that some of notches appear to contain 3 bristles. Full-length false tibial combs lacking and rarely with even the appearance of one on apical ½.

GENERIC DESCRIPTION. Head in general resembling *Medwayella* and *Lentistivalius* but somewhat longer and bearing more bristles. Head rounded and somewhat recurved in ♂ (fig. 164); "frontal" region here somewhat less than thrice as high (vertex to ventral margin) as long at level of uppermost bristle of row II, and about twice as long at level of eye bristle; in ♀, corresponding figures are about 2·5 and 1·6–2 times, respectively. With head-bristles slender; preantennals in 4 rows but with several supernumeraries, which may appear like a fifth row. Eye large, reniform, with sinus ventral, subcaudal and subventral in position, just above apex of procoxa. Eye bristle (E.B.) inserted above level of eye, but in ♂, with caudalmost bristle of row IV just in front of eye. Ultimate (fifth) segment of labial palpus reaching apex of procoxa, or nearly so. With 3 rows of postantennal bristles, plus the usual 1 midway between last 2 rows, near antennal groove.

Pronotum dorsally subequal to, or slightly exceeding, length of adjacent spines of comb; with 2 rows of bristles, first row incomplete; comb with a total of 22–24 spines, and these narrow, somewhat oblique and bluntly pointed. Mesonotum with 4 regular rows of bristles but anteriorly crowded with smaller bristles that may constitute 1–2 additional rows; the greater number occurring in ♀, with 1 subdorsal pseudoseta. Metanotum with 3 regular rows of bristles plus a more anterior incomplete row. Mesepisternum with about 4–5 bristles; mesepimere 5–6. Lateral metanotal area somewhat higher than long; with a dorsocaudal long bristle. Metepisternum with a dorsocaudal bristle. Squamulum short and broad in some species; long and thin in others. Metepimere usually with 12–13 bristles in 3 rows, and some of last row accompanied by 1–2 small intercalaries. Tibiae with 7 groups of stout dorsomarginal bristles (including apical one); in pro- and mesotibiae, usually with 4 groups containing 3 stout bristles each. Metatibia with at least 5 distinct notches containing dorsomarginals and these generally with 2 stout bristles and with 1–2 of subspiniform type below the notch; lacking full-length false combs, and in only one species (*S. aporus* Jordan & Rothschild, 1922) does even apical ½ appear comb-like. Fifth tarsal segment with 6 pairs of plantar bristles, of which fourth pair (from base) somewhat displaced towards midline; in pro- and mesotarsi, first pair may also be slightly displaced. None of tarsi with apical bristles extending beyond middle of next segment (except perhaps for distalmost of fringe of segment 1 of protarsus in both sexes). Proportions of tarsal segments essentially as that noted for *Medwayella dryadosa*.

First abdominal tergum with 4 rows of bristles, remainder of unmodified abdominal terga with 2 ½ rows in ♂, 3 in ♀; ventralmost bristle of caudal row below spiracular fossa. Terga 2–5 with 1 apical spinelet on each side. Basal abdominal sternum without setae in ♂, although these often represented by 6–9 microsetae or their bases; in ♀ with about 16–24 small bristles in 2 or 3 highly irregular, oblique or subvertical rows, commencing subdorsally near anterior margin and extending submedially to about ventral ⅕, at caudal ⅓; ventralmost bristles accordingly the most

caudal. Representative sterna in ♂ with a caudal row of 3 long subventral bristles, at times surmounted by a small submedian one; with an additional 2 short rows of small subventrals preceding this, plus an anterior 1–2 small ventromarginals making a total of 11–16 in all; in ♀ with about 18–20 bristles in same general pattern but more bristles per row, generally including 5 long bristles in caudal row. Tergum 7 in ♂ with a short dorsal lobe (fig. 165, U.L.7) extending between the sets of antepygidial setae (A.B.); in ♀, both upper lobe (fig 166, U.L.7) and lower lobe (L.L.7) well developed and acute. Three bristles of ♀ 7 T. modified so as to somewhat resemble A.B. and somewhat displaced thereto; uppermost (U.M.B.) at times quite similar to upper A.B., first of lower such (L.M.B.) often contiguous to plate of A.B. and closely resembling upper A.B., generally more so than second (L.M.B.-2). Dorsal A.B. about $\frac{1}{2}$ length of ventral one in ♂; usually slightly longer than $\frac{1}{2}$ in ♀.

Male. Tergum 8 reduced; resembling that of *Medwayella*. Sternum 8 relatively unmodified, lacking a group of close-set bristles or spiniforms; very large, enclosing most of genitalia; extending dorsad to base of anal segments and cephalad to level of base of A.B.; about 1·4 times as long (near ventral margin) as high at maximum level (at cephalodorsal angle). Dorsal margin of 8 T. fairly straight to caudal $\frac{1}{4}$ or beyond; and in some species horizontal; in others, oblique at about angle of 30°; ventral margin varying inversely regarding slope so that narrowing effect is the same, viz., caudal margin about $\frac{1}{2}$ height of cephalic. Manubrium (fig. 165, MB.) broad all the way to near apex; ventral margin biconvex near middle; with a short dorsal distal tubercle. Immovable process of clasper (P.) broadly rounded apically. Conical process (C.P.) fairly broad, at times about 5 times as tall as broad at middle; but in some taxa only about 3 times. Movable finger (F.) very long and thin, about 6·5–7 times as long (from apex of P.) as broad near base of distal fringe (D.FR.), narrowed for most its length; apical margin quite flat. Stiva (STV.) fairly long and narrow. Distal fringe (D.FR.) of about 6–8 bristles commencing on shaft of F. and proceeding onto STV. Sensilla-group (S.G.) consisting of 3 short bristles. Fulcral sclerite (F.S.) higher (longer) than broad; subvertical; broadest at dorsal end; narrowest subventrally. Proximal arm of sternum 9 subvertical; with basal $\frac{2}{3}$ at angle of about 60°; uppermost nearly perpendicular; upper $\frac{1}{3}$ of caudal margin biconcave. Distal ("horizontal" or "ventral") arm of sternum 9 (figs. 167–169, D.A. 9) broad; angled caudad dorsally by virtue of a large mesal flap or extension, the apicocaudal flap (AC.F.9) which is fringed with subspiniforms; apex or subapical region of straight upright portion lobate (A.LB.9) and clothed with thin marginal bristles; with a short apical or subapical, anterodirected spur. D.A.9 apparently with ventral margins fused to about apical third at level of marginal transverse sclerotization (T.S.).

Aedeagal apodeme resembling manubrium for most its length, though broader at apex and lacking an apical tubercle or spur. Its middle lamina (figs 170, 174, M.LAM.) about 3·3–3·6 times as long (to near anterior end of crescent sclerite (C.S.)), or caudal margin of lateral shafts of capsule (L.S.C.) as broad at anterior margin of its bay (B.M.L.). Lateral laminae (L.LAM.) lightly tanned and most noticeable at anterior end, where each extends ventrad of M.LAM.; with ventrocaudad extensions arising from dorsum, near anterior end of B.M.L., and crossing bay but scarcely

discernible until underlying proximal arm of sternum 9 (P.A.9), and here appearing as a well tanned line (blending with extensions of girdle (G.) of wall of aedeagal pouch) which continues across M.LAM. to base of Y-sclerite (Y.S.), where it meets the virtually inapparent ventral margin. Ventral wall of aedeagal pouch (AE.P.-V.) well sclerotized, extending to base of body of crochet (B.CR.). Median dorsal lobe (M.D.L.) evenly curved; gradually arching dorsad from level of base of sclerotized inner tube (S.I.T.); height of convexity near level of base of Ford's sclerite (F.SC.) and here only slightly arched. Hood (HD.) relatively tall (long) and narrow; its ventral margin continuing cephalad as the deltoid flap (DEL.FL.) to about level of middle of B.CR.; here DEL.FL. curving dorsad (at times recurving dorsocaudad) to level of pivotal ridge (PIV.R.), in line with base of phylax (PHY.). Anterodorsal angle of DEL.FL. not highly acuminate. Lateral lobes greatly reduced; inapparent. Sclerotized inner tube (S.I.T.) generally so greatly elongated as to be vermiform; apical $\frac{2}{3}$ or $\frac{1}{2}$ arched to form a semi-ellipse; at least 7–12 times as long as broad at middle, and a minimum of 5 times as long as broad at base of phylax; usually 11 times as long as broad at phylax and in some instances, more than 20 times as long as broad. S.I.T. characterized by a sclerite which arises ventrally near its base and loops around the sides of the tube, and which is herein termed lateral wings of ventral armature (L.W.AR.). S.I.T. with a short protrusion from apex (figs 170, 171, FIS.) equivalent to girth of lumen of S.I.T. and dorsally somewhat tanned, appearing as if an extension of a tube within a tube and regarded as comparable to the "fistula" (Peus, 1956), or "outer part of inner tube" (Holland, 1955) or "band of inner tube" (Traub, 1950) associated with ceratophyllids, etc., although much shorter in *Stivalius*. Ford's sclerite (F.SC.) massive, the largest structure in the endchamber; usually flask-shaped or at least constricted subapically; with 1 or 2 claw-like apices (in lateral aspect); not differentiated into securifer and alpha-portions. Phylax (PHY.) well developed as a large sigmoid or bowed sclerite crossing over S.I.T. near base and extending to level of lightly tanned pivotal ridge (PIV.R.), but well anterior to base of F.SC. Pivotal chord (PIV.CD.) feebly sclerotized. Crochet notable in virtually complete reduction of ventral arm, and hence lacking a crochet-process or paramere-like structure. Body of crochet (B.CR.), the upright arm of crochet of other related taxa, well represented, however; relatively long and narrow; base extending from ventral portion of endchamber; apex flattened and expanded, at base of F.SC.; at times (e.g., *S. phoberus*) with a ventral, short, caudad-directed spur, probably representing a vestige of crochet-process. Crescent sclerite (C.S.) large; apex within base of S.I.T. and hence satellite sclerite (SAT.S.) wholly within. Fulcral lateroventral lobes (FUL.L.L.) short. Central sclerite (CEN.S.) appressed to fulcral medial lobes (FUL.M.L.). Lateral shafts of capsule (L.S.C.) well tanned. Y-sclerite (Y.S.) very large; both components visible in mounted specimens. Vesicle (V.) and ventral virga (V.V.) well developed. Penis rods short, scarcely reaching anterior end of apodeme when *in situ*. Third apodemal rod (AP.R.) of endophallus and dorsal virga (D.V.) lightly tanned, especially the latter. Caverna spiculosa (CAV.SPIC.) submedian in position and anterior to level of fulcrum.

Female. Spermatheca (figs 176, SP., 163, 177) with bulga (B.) longer than hilla (H.); bulga broader (taller) caudally than anteriorly and at times constricted in

middle; hilla with an apical papilla and somewhat inserted into lumen of bulga. Duct of spermatheca (figs 163, 176–179, D.SP.) with internal striae in dilated portion (DIL.P.) near junction with bursa copulatrix (B.C.), which in turn is thick-walled, very broad most of its length, and generally (fig. 163) markedly involute, or at least coiled or folded upon itself (fig 162), apically, if not elsewhere as well. B.C. with perula not clearly differentiated; with part of inner wall of lumen at times well sclerotized and appearing like a curved band. Wall of roof of oviduct (fig. 163, OV.) well tanned as it (or paired members thereof) approaches vagina (VAG.). Paragenital morion reduced, inapparent; apparently represented by indiscrete lines on each side of B.C., near vagina. Sternum 7 (fig. 175, 7 S.) with ventral $\frac{1}{2}$ of caudal margin biconcave, but upper sinus at times quite small (as in figure). Ventral anal lobe (fig. 176, V.A.L.) with base short; apical margin long; anterior $\frac{1}{3}$ of margin somewhat convex and bearing 4–5 close-set, long bristles; remainder of margin sinuate, bearing 2 long bristles at apical $\frac{1}{3}$ or $\frac{1}{4}$. Anal stylet (A.S.) long and narrow, parallel-sided and lacking long subapical bristles. Mesal genitalic ridge of tergum 8 undeveloped. Tergum 8 (8 T.) with a short lobe at ventrocaudal angle. Spiracular fossa 8 (fig. 166, 8 SPC.) medium-sized; upright portion ovate, not much longer than broad. Sternum 8 (8 S.) flask-shaped and with short apical bristles.

Comment. Species included: (1) *S. ahalae* (Rothschild, 1904), the type of the genus; from rats, south India; (2) *S. aporus* Jordan & Rothschild, 1922, from *Rattus*, *Millardia* and other murines from Ceylon, India and Nepal. (A subspecies of *aporus*, or a closely related new species, occurs in Thailand and Vietnam on rats.) (3) *S. phoberus* Jordan & Rothschild, 1922, from rats in Ceylon. (4) *S. c. cognatus* Jordan & Rothschild, 1922, *from Rattus* (*Rattus*) in Java; *S. c. spiramus* Jordan, 1926 (new status), from *R.* (*Rattus*) in the mountains of Luzon, Philippines, and the new subspecies next described, from *R.* (*Rattus*) in the mountains of Mindanao, Philippines. (5) *S. rectodigitus* Li & Wang, 1958. Even though the authors state this is near *S. klossi* Jordan & Rothschild, 1922, and compared it with that species, it definitely is close to *S. aporus* (and may be a subspecies thereof) and hence is a member of *Stivalius s. str.*, while *S. klossi* belongs to a separate and yet un-named genus. The status of *S. rectodigitus* is clear, as indicated by Li & Wang's figures of the bursa copulatrix and of the distal arm of the ninth sternum, etc. Further, those authors point out the aedeagal similarities with *S. aporus*.

Further discussion of the genus is presented after the treatment of *S. cognatus* below.

1. ***Stivalius cognatus*** Jordan & Rothschild, 1922

Stivalius cognatus Jordan & Rothschild, 1922. Ectoparasites I : 253, 264, figs 243, 245; Jordan, 1933, Novit. zool. 38 : 355; Costa Lima & Hathaway, 1946, Pulgas: 326; Traub, 1951, Proc. biol. Soc. Wash. 64: 13; Smit, 1958, Bull. Brit. Mus. (Nat. Hist.) Ent. 2(2): 41.

Diagnosis. Immovable process (fig. 165, P.) very short and broadly rounded at apex; with a small subapical caudomarginal bristle. Movable finger (F.) with portion above apex of P. about 6·3 times as long as broad at level of ventralmost bristles of distal fringe (D.FR.); slightly narrowed near basal portion of D.FR., otherwise margins quite straight and parallel; apex subtruncate. Stiva (STV.) of F. well

developed; longer than unexpanded portion of apex and about 2·7 times as long as broad. Sclerotized inner tube (figs 170, 173, S.I.T.) elongated, but not nearly as long as in *S. ahalae* and *S. aporus*, i.e., extending only slightly beyond apex of F.SC., instead of for more than $\frac{1}{4}$ its length; with its arc paralleling that of median dorsal lobe (M.D.L.) instead of being much more complex. Ford's sclerite (F.SC.) narrowed near middle of sclerite, flask-like; with basal portion (proximad of dorsal spur or peak) subequa' to portion distad, instead of being $\frac{2}{3}$ length of neck of flask. Basal portion of F.SC. only 1·7 times as long as broad at level of dorsal spur instead of 3·5 times. Distal arm of sternum 9 (figs 167–169, D.A.9) with only one spur on anterior (dorsal) margin, occurring at base of apical rounded lobe (A.LB.9), which in turn is not as high as long, instead of vice versa. Sinus above ventral lobe of ♀ sternum 7 (figs 163, 176, 7 S.) somewhat similar in size and shape to that of lobe below it. Bursa copulatrix (figs 163, 177) with convolute portion quite symmetrical in size and shape. Spermatheca (fig. 176, SP.) with bulga (fig. 177, B.) somewhat constricted near middle; caudal $\frac{1}{2}$ more convex dorsally than cephalic portion; slightly more than twice as long as high immediately anterior to constriction (maximum internal measurements); caudal and ventral margins externally quite straight, only slightly convex. Hilla (H.) with about basal $\frac{1}{5}$ inserted in lumen of bulga; somewhat squarely recurved at midpoint and slightly dilated above this curve; about thrice as long as broad near bulge; apex broadly rounded. Apical papil'a (PAP.) about $\frac{1}{3}$–$\frac{1}{2}$ diameter of H.; somewhat longer than broad.

For further details of aedeagus, see section 1.c. below, on new subspecies.

Comments. *S. cognatus*, like other members of the genus (*s. str.*), is a typical parasite of members of the subgenus *Rattus*. The original description was based upon material from Java, but Traub (1951) quoted Karl Jordan, F.R.S., as expressing the belief (in litt.) that *S. spiramus* Jordan, 1926, from Luzon, known only in the female, was the same species. Jordan's perspicacity was demonstrated when the writer collected topotypic material of *S. spiramus* in 1961 and found that the specimens were indeed *cognatus*, but of subspecific rank. This subspecies is described below, along with a new one from Mindanao. Undoubtedly other subspecies, and perhaps related species, occur elsewhere in the Indonesian and Philippine Archipelagoes, and our understanding of zoogeography would be enhanced if such material became available for study.

1. a. ***Stivalius cognatus cognatus*** Jordan & Rothschild, 1922

Diagnosis. Characterized by the following features: (1) Distal arm of sternum 9 (fig. 168, D.A.9) with apical lobe (A.LB.9) about 2·4 times as long as high. (2) Apicocaudal flap (AC.F.9) of D.A.9 about 1·6 times as long (from level of margin of transverse sclerotization, T.S.) as broad at middle. (3) Phylax of aedeagus fairly straight and narrow, about 5 times as long as broad at maximum (at middle); scarcely broader at middle than subapically. (4) Ford's sclerite with total length 1·9 times length of basal section (portion anterior to dorsal angle or nubbin) and about 2·5 times breadth at apex of basal section. (5) Bursa copulatrix (fig. 179, B.C.) with coil oblate, rather flattened dorsally. (6) Vertical diameter of involute portion

exceeding distance from bottom of loop to vagina (VAG.). (7) Lateral metanotal area usually longer than high (internal measurements).

COMMENT. The only published records for the nominate form are those in the original description, viz., from *Rattus* (*R.*) *rattus* (cited as *Epimys rattus*), from Malang, Java. The specimens studied and the female here illustrated, are from an unrecorded area in Java, coll. M. V. Kuhlavain, and determined by the late Karl Jordan, F.R.S., and received through his kind offices.

ILLUSTRATIONS

168. Distal arm of sternum 9
179. Spermatheca and bursa copulatrix

1. b. *Stivalius cognatus spiramus* Jordan, 1926, NEW COMBINATION

Stivalius spiramus Jordan, 1926. Novit. zool. 33 : 391, fig. 12; Costa Lima & Hathaway, 1946, Pulgas: 327; Traub, 1951, Proc. biol. Soc. Wash. 64 : 13.

DIAGNOSIS. (1) Distal arm of sternum 9 (fig. 169, D.A.9) with apical lobe (A.LB.9) about twice as long as high. (2) Apicocaudal flap (AC.F.9) about 1·7 times as long as broad at middle. (3) Phylax (fig. 173, PHY.) symmetrically sigmoid, narrow; about 5 times as long as broad at maximum near middle. (4) Ford's sclerite (F.SC.) 1·6 times as long as its basal portion and 1·9 times as long as broad at apex of proximal region. (5) Bursa copulatrix (fig. 178, B.C.) with involute portion quite circular in outline. (6) Vertical diameter of loop exceeding distance from bottom of coil to level of vagina (VAG.). (7) Lateral metanotal area usually longer than high (internal measurements).

COMMENT. *S. spiramus* was described from, and heretofore known only from, a single female collected by Professor E. H. Taylor at Baguio Bengue (Luzon) from a rat cited by Jordan as "*Rattus guereci.*" (This name probably was a *lapsus* for *querceti* Hollister, 1911, a Luzon rat which is placed by Ellerman (1941) in the *Rattus* (*R.*) *concolor* group but which is treated by Schwarz & Schwarz (1967) as a synonym of *Rattus rattus negrinus* Thomas, 1898.) The present description and figures are based upon specimens which I collected at Baguio, at 3600-4500 ft elev. in October, 1961, ex *Rattus* (*R.*) *rattus* ssp., and which can be considered as topotypic. The allotype ♂ is therefore selected as follows: Allotype ♂ (B-55028) ex *Rattus exulans*; PHILIPPINES: Luzon, Baquio; elev. 3600 ft; 24.X.1961; Coll. R. Traub; deposited in the U.S. National Museum.

ILLUSTRATIONS

169. Distal arm of sternum 9
173. Apical region of aedeagus
175. Sternum 7 (♀)
178. Bursa copulatrix

1. c. *Stivalius cognatus bamus* subsp. nov.

TYPE MATERIAL. Holotype ♂, allotype ♀ (B-56383) ex *Rattus rattus mindanensis*; PHILIPPINES: Mindanao, Zamboanga del Norte, Mt Malindang, Masawan, Mutia; elev. 4500–5000 ft; 29.XII.1962; Coll. D.S. Rabor. Paratypes as follows: Collected

by D. S. Rabor, 24.XII.1962/14–16.I.1963; same locality as holotype; 27 ♂, 36 ♀ ex *Rattus rattus mindanensis*; 2 ♀ ex *R. rabori*; 2 ♀ ex *R. exulans todayensis*; 1 ♂, 1 ♀ ex *R. pantarensis*; 4 ♂, 4 ♀ ex *Apomys insignis bardus*; 1 ♂, 1 ♀ ex *Rattus* sp., Ibid. but elev. 5200–7000 ft; 2 ♂, 3 ♀ ex *R. r. mindanensis*; Mt Malindang, Canon, Mutia; elev. 3200 ft; 22–24.XII.1961.

Holotype (U.S.N.M. number 71610), allotype and 3 pairs of paratypes deposited in the U.S. National Museum. The remainder distributed as for *M. dryadosa*.

Diagnosis. (1) Distal arm of male sternum 9 (fig. 167, D.A.9) with apical lobe (A.LB.9) about 2·6 times as long as broad. (2) Apicocaudal flap (AC.F.9) relatively short and broad, viz., about 1·3 times as long (from level of caudal margin of transverse sclerotization, T.S.) as broad at middle. (3) Phylax (figs 170, 174, PHY.) eccentrically sigmoid; upper ½ narrower than lower ½ and much more curved; relatively broad, i.e., only 3·4 times as long as broad at maximum breadth (below middle). (4) Ford's sclerite (F.SC.) with basal portion (to level of dorsal nubbin) only ½ total length of F.SC. and about 2·6 times breadth of sclerite at level of dorsal peak. (5) Bursa copulatrix (figs 163, 176, 177, B.C.) with upper portion evenly involute; symmetrical. (6) B.C. relatively long, so that vertical diameter of loop is merely equal in length to lower portion of bursa, i.e., from ventral margin of coil to vagina (VAG.), instead of exceeding it. (7) Lateral metanotal area higher than long (internal measurements).

Descriptive Notes. Since the aedeagus of this species has never been described before, further notes are included here, including comments on this organ as seen from the ventral aspect. It should be borne in mind, however, that most of the points (save for those cited in the diagnosis) are on the species level.

Aedeagus—Lateral Aspect (figs 170, 174). Aedeagal apodeme with middle lamina (M.LAM.) about 3·6 times as long (to level of caudal margin of lateral shafts of capsule (L.S.C.) as broad at anterior margin of its bay (B.M.L.). Hood (HD.) with ventral margin shallowly concave save for curves at anterior and posterior margins; lightly reticulated apically; apparently laterally reinforced by transverse parallel light striae, especially over caudal ⅓, which is the deltoid flap (DEL.FL.). HD. and DEL.FL. extending caudad to base of phylax (PHY.) and body of crochet (B.CR.). Median dorsal lobe sloping at about angle of 30° commencing at level of slightly acute anterodorsal angle of DEL.FL.; maximum height of its gentle, broad arc is at level somewhat apicad of Ford's sclerite (F.SC.) and thereafter sweep of curve paralleling that of dorsal margin of F.SC. (if not pivoted out of position). Aedeagal pouch (AE.P.) with ventral border well tanned; but anterior wall (girdle, G.) less so, and with its cephalodorsad extensions soon meeting the ventrocaudal prolongations of lateral laminae (L.LAM.). Ford's sclerite (F.SC.) with length almost equal to that of body of crochet (B.CR.) and quite broad for proximal ½, which resembles base of a flask; basal ½ with dorsal and ventral margins fairly straight and parallel; narrowed portion of flask slightly more than ½ length; lower margin sinuate. F.SC. with breadth of middle region of anterior ½ equal to that of basal part of sclerotized inner tube

(S.I.T.); apex oblique and subtruncate, terminating in a ventrocaudal projection. S.I.T. with apical $\frac{2}{3}$ curved in arc almost paralleling that of M.D.L. but extending more distad, to a level slightly beyond apex of F.SC.; approximate breadth of middle of tube slightly more than $\frac{1}{3}$ of that of subapical region of F.SC.; about 10–14 times as long as broad at level immediately proximad of B.CR. Lateral wings of ventral armature (L.W.AR.) somewhat ovate, but narrower dorsally than ventrally and reaching to near dorsal margin of S.I.T. Crescent sclerite fairly long; with a preapical anterior hump; narrowed caudally and with caudal $\frac{1}{3}$ penetrating S.I.T. where it is virtually contiguous with angled, relatively long satellite sclerite (SAT.S.). Central sclerite (CEN.S.) closely appressed to fulcral medial lobes (FUL.M.L.) and resembling acute wing of an arrowhead. Y-sclerite (Y.S.) with one fork narrow, horizontal and extending to level of base of SAT.S.; larger fork very conspicuous as a diamond-shaped sclerite below fulcrum. Dorsal virga (D.V.) indistinct. Phylax (PHY.) a fairly broad, bowed sclerite which is upcurved below midpoint and somewhat narrowing apically, about 2·3 times as long as broad at maximum girth (below middle) (distinctly narrower in other subspecies). Body of crochet (B.CR.) ribbon-like except for flattened, expanded apex; axis flattened except for somewhat concave extremities; ventrally projecting somewhat below S.I.T. as a narrowed, acute rod, this portion presumably representing a vestige of the crochet-process (paramere) of other genera. Lacking discernible tanned lateral connections between AE.P. and B.CR., with what is apparently a small seta on apical margin of AE.P., on each side, at base of B.CR. and of PHY. With the upper penis rod (P.R.) extending to near level of anterior end of aedeagal apodeme when *in situ*; lower rod much shorter. Ventral virga stout; sclerotized for entire length, viz., to near level of base of bay of middle lamina. Third apodemal rod (AP.R.) lightly tanned once leaving AE.P. Caverna spiculosa (CAV.SPIC.) irregularly ovoid; about twice as long as broad; sloping cephaloventrad at an angle of about 60°.

Aedeagus—Ventral Aspect (fig. 171). Hood with anterior margin entire, lightly tanned. Ford's sclerite shaped like a tulip flower, about 1·3 times as long as broad near base; without any caudad-directed paramere-like structures; the hook-like apex of the lateral aspect actually representing a deep structure extending all the way across the sclerite which is seen on edge. Deltoid flap (DEL.FL.) covering only sides of ventral margin. Phylax (PHY.) actually with base (ventral) fairly narrow and constricted; straddling S.I.T. and apices meeting dorsally above it; therefore projection of PHY. in ventral aspect is that of a trapezoid with thickened sides. Body of crochet (B.CR.) dorsally buttressed against base of F.SC. S.I.T. appearing as a long, narrow cylinder whose only modifications are an apex that is slightly recurved ventrad, viz., the fistula (FIS.), and a narrow, basal belt, viz., the lateral wings of the armature (L.W.A.R). Wall of aedeagal pouch well tanned both laterally (AE.P.-L.) and ventrally (AE.P.-V.); lacking sclerotized connections with body of crochet (unlike the condition in pygiopsyllids with ventral crochet-processes). Vesicle (V.) quite large, and ventral virga (V.V.) broad. Y-sclerite (Y.S.) with bifid anterior base and broad caudal stem flooring middle of capsule, which is quite broad, distance between fulcral lateroventral lobes (FUL.L.L.) nearly equal to length of fulcral area. Caverna spiculosa (CAV.SPIC.) lateral in position.

Comment. (1) The vast majority of records of *S. c. bamus* are from *Rattus rattus mindanensis*, with a few from the related murine *Apomys*, all from Mt Malindang at elevations between 3200–5000 ft. As yet material from other parts of Mindanao is unavailable for study, so that the true range of the subspecies is unknown, and also it cannot be stated that this is the only subspecies of *S. cognatus* occurring on the island.

(2) *The aedeagus of S. cognatus.* The structure of the aedeagus as seen in the ventral aspect emphasizes and clarifies some of the points made above, in the consideration of the genus. Thus, the lack of overt connections between the walls of the aedeagal pouch and the crochet is quite striking and is in marked contrast to related taxa. The difference seems to be associated with the presence of a well developed quasi-crochet or ventral crochet-process: if these are present, as in *Medwayella* and *Lentistivalius*, there are definite links between the crochet and the pouch wall; if absent, as in *Stivalius s. str.*, there are no discernible ties. It also is apparent that Ford's sclerite does not bear a pair of narrow hooks or prongs, as one might infer from the lateral aspect. Instead, the apex bears a downward directed flange or lip which extends from one side to the other, and which presumably acts like a prying lever when F.SC. is pivoted ventrad.

Bristles or bristle-like structures are virtually unknown on the aedeagus, and the few isolated examples known to me were regarded as atavisms or freaks. However, the fine seta on each side near the caudoventral margin of the pouch wall in *S. cognatus* can be seen in most specimens and even seems to arise from an alveolus. Since many of the components of the phallosome of fleas are paired, it seems logical to assume the organ is derived from an ancestral bilaterally symmetrical structure, and that this had borne bristles. If so, a setal vestige is not surprising and is in accord with my belief that pygiopsyllids are in general primitive fleas despite certain adaptive specializations, which at times are quite marked.

(3) Abnormal structures of fleas are often of interest in that they may represent atavisms or anomalies that suggest the origin of the normal organ. A freak bristle is therefore labelled FRK. in fig. 165, although no further comments can be made at this time on its possible significance.

Illustrations

163. Spermatheca and genitalia (♀)
164. Head and prothorax (♂)
165. Processes of clasper
166. Antepygidial region (♀)
167. Distal arm of sternum 9
170. Apical region of aedeagus (lateral)
171. Apical region of aedeagus (ventral)
174. Apical region of aedeagus
176. Spermatheca, genitalia and anal segments
177. Spermatheca and bursa copulatrix

2. Comments on *Stivalius s. str.*

Host-Relationships, Distribution and Potential Vectorship of Disease.

Throughout its known range (Ceylon, Indian Subcontinent, S.E. Asia, Indonesia and the Philippines) the genus *Stivalius s. str.* is primarily associated with murine rodents, especially the subgenus *Rattus*. Blood-sucking ectoparasites of murines are of special interest regarding transmission of disease, but the role of *Stivalius s. str.*

in this regard is in need of clarification. *Stivalius cognatus*, reported as *Pygiopsylla ahalae* in Java according to Pollitzer & Meyer (1961), and, *Stivalius* species "have been found capable of transmitting plague in Java and south India" respectively (Pollitzer, 1954). Inasmuch as the studies referred to by Pollitzer concern *Stivalius* from rats, the species in question are almost undoubtedly members of *Stivalius s.str.*, e.g., *S. ahalae*, *S. cognatus* and *S. aporus* (or *S. phoberus*, if it occurs on the mainland and not merely Ceylon), since the only other Indian "*Stivalius*" is the species referred to above, in the present paper, as *Lentistivalius ferinus*, and is a parasite of shrews. The role of *Stivalius* in the ecology of both human and murine plague needs elaboration especially since this disease is still endemic in areas where plague exists today in Indonesia, Thailand and Vietnam and where members of this genus are known to, or may be expected to infest *Rattus* (*Rattus*). The possible involvement of *Stivalius s. str.* in the ecology of murine typhus should be investigated, for this flea-borne disease is likewise associated with the subgenus *Rattus* and is endemic, or presumed to occur, in regions where *Stivalius s. str.* infests commensal rats.

The Specialized Aedeagus and Bursa Copulatrix

Stivalius s. str. exhibits some remarkable genitalic modifications that are not seen in related taxa, many of which have developed other complexities in the sexual apparatus. The marked elongation of the sclerotized inner tube (figs 170–171, 173–174, S.I.T.) is quite striking as compared to *Lentistivalius*, for example (fig. 172). Moreover, the apex of S.I.T. is further specialized in *Stivalius s. str.* by the apically protruding, somewhat tanned fistula (fig. 170, FIS.). There are scores of species referable to *Stivalius s. lat.*, and it can be no coincidence that females in which the bursa copulatrix is broad, sausage-like and coiled (and no others) are the mates of males with snake-like aedeagal tubes. Such parallel developments in the two sexes of *Stivalius s. str.* in the course of evolution strongly suggest a functional and fundamental relationship, namely that, in this taxon, unlike the case in most fleas, S.I.T. itself, and not merely the penis rods,[15] enters well into the bursa. This then would explain the thickened walls of the bursa and the sclerotized rod-like lining of one side of the lumen of the bursal duct seen in this genus.

Two points are mentioned here as rendering support to this hypothesis. The characteristic absence of ventral "parameres" in *Stivalius s. str.* indicates that the function of the caudad-directed, finger-like or rectangular crochet-process (CR.P.) of related taxa has been taken over by some other structure. The crochets of ceratophyllids, leptopsyllids and some other fleas serve to secure and maintain a hold on

[15] Holland (1955) reiterated the view of Snodgrass (1946) that the penis rods ". . . are the only elements of the intromittant apparatus that are capable of being protracted from the aedeagus . . ." When Holland (p. 245) speaks of the "long outer part of the aedeagal inner tube" (not to be confused with sclerotized inner tube) as being "inserted well within the bursa copulatrix," and other writers make similar statements, they are referring to a structure that is regarded as already being *outside* of S.I.T. Thus, there is no contradiction, for the outer tube is not being protracted from S.I.T. This outer tube is the structure referred to above as the fistula (FIS.).

Moreover, it should be borne in mind that Snodgrass, Traub (1950), Holland, Goncharov (1964 a & b) and others, when discussing the copulatory apparatus or copulation in Siphonaptera, were referring to specific taxa of fleas and their observations do not necessarily apply to other fleas. Pygiopsyllids and rhopalopsyllids in particular have not been studied in this regard.

the female genitalic apparatus and to open some of the components to the male organs (Holland, 1955, Goncharov, 1964). Presumably the unusually well developed Ford's sclerite (F.SC.) of *Stivalius s. str.* assumes some of these functions in the absence of the crochet-process, as is suggested by the hook-like appearance of its apex (fig. 170), which, as can be seen in ventral aspect (fig 171) is really a down-projecting flange and which presumably acts as a pry when the apex of F.SC. is tilted ventrad. It also seems logical to believe that the hypertrophied and specialized S.I.T. takes over other functions, especially since there are instances within the Order wherein the aedeagal tube apparently is the true penetrating copulatory organ, and not the penis rods. Thus, Barnes and Radovsky (1969) cite impressive morphological evidence for this belief, in the case of *Tunga* Jarocki, 1838, and Suter's figures (1964) of copulating *Tunga* seem to bear this out. The second point suggesting that these modifications in the male and female of *Stivalius s. str.* are correlated, is the illustrative case of *S. phoberus* Jordan & Rothschild, 1922. Here S.I.T. is not as narrowed and elongated as in other species of the taxon, i.e., it is only 5 times as long as broad at level of phylax, instead of 9–20 times. In this species (fig. 162) the bursa is not as modified either: it is less involute and not quite as broad throughout (*cf.* fig. 163, *S. cognatus bamus*).

In *Medwayella* and *Lentistivalius*, which possess well developed caudad-directed ventral crochet-processes, there are obvious tanned connections between the wall of the aedeagal pouch and the crochets. It is noteworthy that in *Stivalius s. str.*, which lack ventral "parameres" and crochet-processes, such bonds are inapparent, even in the ventral aspect (fig. 171), as is pointed out below.

A test of this hypothesis may be provided by another group of pygiopsyllid fleas in which the basal half of the bursa copulatrix is very broad and thickened, namely the three species of *Acanthopsylla* Jordan & Rothschild, 1922, in which there is but 1 (not 2 or 4) spiniforms on the frontal region of the head, viz. *A. praxilla* M. Rothschild, 1934, *A. guba* Smit, 1953 and *A. richardsoni* Smit, 1953. In the other members of the genus (which includes a total of 16 species), the ventral portion of the bursa is not conspicuously dilated and lacks ring-like striations. In these 13 other species, the sclerotized inner tube of the aedeagus is not elongate, corresponding to the relative size typical for the bulk of the pygiopsyllids. In the *A. praxilla*- group the male is known only for one species (*A. richardsoni*), which I have not seen, and its aedeagus has never been figured. However, the shape of the bursa copulatrix in this group of fleas is so suggestive of the condition in *Stivalius s. str.* that I expect that here too the sclerotized inner tube of the male must be elongate, if not ophidian in shape, and that ventral crochet- like processes are lacking.

Evolutionary Status of Stivalius s. str.

It is noteworthy that this taxon, which is the most highly specialized of this group of pygiopsyllids with respect to modifications of the aedeagus and the co-functional bursa copulatrix, consists of characteristic parasites of the subgenus *Rattus*, the most modern and highly developed of the murines. This suggests that *Stivalius s. str.* is likewise at the pinnacle of the evolutionary development of this complex of genera to date. These points are discussed further in the two following articles in the series.

3. Key[16] to the known species and subspecies of STIVALIUS Jordan & Rothschild, 1922, *s. str.*

1 Male with scolerotized inner tube of aedeagus (figs 170, 173, S.I.T.) at least 9 or more times as long (from base) as broad at base of phylax (PHY.) and 20–30 times as long as broad at middle. Female with bursa copulatrix (figs 163, 178, B.C.) markedly involute, the coil(s) quite symmetrical and not overlying vertical (ventral) portion of tube; often large, involving most of length of bursa. (Indian Subcontinent to Philippines) 2

Sclerotized inner tube only about 5 times as long as broad at base of phylax and about 9 times as long as broad at middle. Bursa copulatrix (fig. 162, B.C.) folded upon itself at upper ⅓, the loop asymmetrical. (Ceylon) . . ***phoberus*** J. & R., 1922

2 Arc of S.I.T. (figs 170, 173) shallow, equivalent to curve of median dorsal lobe (M.D.L.), extending only slightly beyond apex of Ford's sclerite (F.SC.), i.e., only for a distance equivalent to less than ½ its total length. Basal portion of F.SC., i.e., region proximad to subapical constriction and below nubbin (peak or spur) on dorsal margin, equals about ½ length of F.SC.; this section only 1·7 times (or less) as long as broad at level of spur. Distal arm of sternum 9 (figs 167–169, D.A.9) with only one spur on anterior (dorsal margin, and that at base of apical rounded lobe (A.LB.9)). Subventral sinus of ♀ sternum 7 (figs 163, 176, 7 S.) almost an inverted and reversed image of ventral lobe, its dorsal margin continuing caudad to or beyond level of margin of ventral lobe before turning dorsad. Ventral lobe of 7 S. narrower than basal part of sinus above it. (Indonesia and Philippines) ***cognatus*** subsp. 5

– S.I.T. with arc much more convex than M.D.L. and equivalent to ½ a broad ellipse, extending beyond apex of F.SC. by more than ¼ its length. Basal portion of F.SC. at least ¾ length of F.SC. and at least 3·5 times as long as broad at level of nubbin (peak or spur) on dorsal margin. D.A.9 with 2 spurs on anterior (dorsal) margin; the additional one proximad of that at base of apical rounded lobe. Subventral sinus of ♀ 7 S. incomplete, not shaped like ventral lobe due to its dorsal margin being more oblique than ventral one or else sharply curving dorsad near base of sinus. Ventral lobe of 7 S. broader (taller) than basal part of sinus above it. (Indian Subcontinent and Ceylon or Yunnan or Southeastern Asia) 3

3 Dorsolateral bristles of hind-tibia with bristles of groups dissimilar in size, the groups fairly widely separated from one another so that there is no resemblance to a comb. S.I.T. extremely long and narrow, at least 18 times as long as broad at base of phylax. F.SC. with only 1 apical prong. Phylax greatly dilated at middle; both margins here convex; only about 2·4 times as long as broad at middle. ♀ 7 S. with upper angle of dorsal sinus acute and projecting as a short thumb ***ahalae*** (Roths., 1908)

– Dorsolateral bristles of hind-tibia with inner members of groups often similar in size and girth and so arranged that apical ½ of tibia bears a nearly perfect comb. S.I.T. elongate, but not so markedly, about 15 times as long as broad at base of phylax. F.SC. with 2 apical prongs. PHY. with only anterior margin convex at middle; about thrice as long as broad at middle. ♀ 7 S. with upper angle of dorsal (lateral) sinus short, not projecting as a thumb 4

4 Distal portion of F.SC. (apicad of nubbin) relatively broad, only about twice as long as broad. Notch at apex of F.SC. with prongs converging somewhat at tip. Seventh sternum of female with lobe above subventral sinus extending more

[16] Only one character per couplet need apply, since these are not combinations of characters. Several alternates are cited to ease identification.

caudad than does ventral lobe; this median lobe smaller than ventral lobe. (Yunnan, Indo-China, Thailand) . . . . . ***rectodigitus*** (Li & Wang, 1958)[17]

– Distal portion of F.SC. narrow, about thrice as long as broad. Notch at bifid apex of F.SC. with prongs diverging at tip or, at most, parallel. Seventh sternum of female with median lobe subequal in size and extent to subventral one (Indian subcontinent and Ceylon) . . . . . ***aporus*** Jordan & Rothschild, 1922

5 PHY. (figs 170, 174) relatively broad, about 2·3 times as long as broad at maximum level. Apicocaudal flap (AC.F.9) of D.A.9 relatively short and broad, viz., length (from level of caudal margin of transverse sclerotization, T.S.) only about 1·3 times breadth at middle. B.C. (fig. 177) relatively long, viz., vertical diameter of involute portion equal to distance from bottom of loop to vagina (VAG.). The portion of wall of B.C. which is anterior to tanned lining of lumen, broader than wall of opposite side of duct. Lateral metanotal area with internal dimensions taller than long at subdorsal level. (Mindanao) ***cognatus bamus*** subsp. n. (p. 287)

– PHY. (fig. 173) narrow; about 5 times as long as broad at maximum level. AC.F.9 (figs 168, 169) comparatively longer and narrower, at least 1.6 times as long as broad at middle. B.C. (figs 178, 179) with vertical diameter of involute portion exceeding distance from bottom of loop to vagina (VAG.). Portion of wall of B.C. which is anterior to tanned lining of lumen, narrower than opposite wall. Lateral metanotal area generally longer than high (internal measurements). (Java and Luzon) 6

6 F.SC. (fig. 173) proportionately short and broad; total length only about 1·6 times as long as its basal portion (to level of dorsal nubbin) and 1·9 times as long as broad at level of dorsal spur. PHY. symmetrically sigmoid. Apical lobe (fig. 169, A.LB.9) of D.A.9 relatively tall, only twice as long as high. B.C. (fig. 178) with involute portion quite circular in outline. (Luzon) ***cognatus spiranus*** Jordan, 1926 (p. 287)

– F.SC. relatively long and narrow; about 1·9 times length of its basal portion and about 2·5 times as long as broad at apex of basal section. PHY. quite straight, definitely not sigmoid. A.LB.9 (fig. 168) proportionately short, about 2·4 times as long as high. B.C. (fig. 179) with involute portion oblate, rather flattened dorsally. (Java) . . . . . ***cognatus cognatus*** J. & R., 1922 (p. 286)

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[17] *S. rectodigitus* was described from specimens from Yunnan. I have seen only specimens from Thailand, Vietnam and Laos, which closely resemble the figures and description of Li & Wang, but which I had regarded as subspecies of *S. aporus*. Further study, including specimens from Yunnan, are required to clarify the status of *S. rectodigitus*, but I am inclined to consider it a subspecies of *S. aporus*. Also, the key-characters cited above for the separation of the females may prove unreliable, but females of related forms of *Stivalius s. lat.* are often difficult or impossible to identify in the absence of associated males.

North Borneo as members of USAMRU in 1951 or 1953 included Capt. C. L. Wisseman, Jr., M.C.,[18] David H. Johnson, Ph.D. (Smithsonian Institution), Charles Wharton, Capt. H. D. Newson, M.S.C., and Capt. B. C. Walton, M.S.C. Scientists from DMZ-IMR on those or other trips to Borneo (i.e., 1953, at Mt. Trus Madi) included Dr. J. R. Audy and Dr. J. L. Harrison, who also were responsible for the DMZ-IMR collections from 1947 onwards, for 10 or more years. B. L. Elisberg, M.D., H. E. McClure, Ph.D., Lt. V. J. Tipton, M.S.C., participated in the USAMRU studies in Malaya at various times. Integral members of the field-teams in Malaya, N. Borneo and Sarawak (1958) were Ben Ensoll and Phang Ong Wah (USAMRU) and Lim Boo Liat and M. Nadchatram (DMZ-IMR). Yoon Yuen Fat and Ng Cheong Kee served on some of the USAMRU trips in Malaya and the latter worked on Tioman Island with UM. The USAMRU teams were all field-units of the Walter Reed Army Medical Center, Washington, D.C.

The accomplishments of Lord Medway's expedition to Gunong Benom are amply attested throughout this volume, but Lord Medway also helped us obtain valuable specimens from other parts of Malaya and North Borneo as well. Dr. J. A. Bullock (UM) was most helpful in providing fleas from northern Malaya and Tioman Island. The Bernice P. Bishop Muesum, via J. L. Gressitt, Ph.D., sent for study, specimens from Java collected by J. M. Stusak. R. E. Elbel, who served with Dr. Audy in N. Borneo in 1953, also collected the bulk of the Thai specimens, while with the U.S. Operational Mission to Thailand. Additional Thai material was provided by Lt.Col. J. E. Scanlon, M.S.C., and other members of the U.S. Component of the SEATO Medical Research Unit in Bangkok. Dr. Boonsong Lekagul was extremely helpful during all the studies in Thailand, as was Kitti Thonglongya.

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F. G. A. M. Smit of the British Museum (Natural History), rendered great assistance by lending me paratypes and unidentified specimens from the Rothschild Collection of Fleas, thereby providing us with a new species for description, while another new species was received from the Director of the Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands. Mr. Smit was also very helpful in determining some of the precise localities in Malaya, Java and Sumatra where specimens in the N. C. Rothschild Collection had been collected.

The illustrations in this series of articles were prepared by members of our Department at Baltimore. Of the photographs 93 are the work of J. Navarro, while Mrs. Suzanne L. Shipley prepared 33 photographs or drawings, including the difficult figures of the dorsal or ventral aspects of the aedeagus. Thirty-three of the illustrations were drawn by Mrs. Avonne Green. The bulk of the figures of *L. vomerus* were prepared by Miss Ermona McGoodwin, but those of the male genitalia are composites made by her and R. Traub. The dissections were prepared by the latter and mounted by Mrs. Phunthong Malikul. Miss Helle Starcke and T. M. Evans rendered considerable editorial assistance.

[18] The military rank cited in each instance is that borne at the time the work was done.

The mammals were identified by J. L. Harrison and Lim Boo Liat (for Malayan and Bornean mammals), Lord Medway (Malaya), D. H. Johnson (N. Borneo and Thailand), Kitti Thonglongya (Thailand for SEATO) and R. E. Elbel (some Thai hosts). With respect to names of hosts, Lord Medway's book on Bornean mammals was followed (1963), as well as Harrison's works on the Malayan (1966) and Bornean (1964) mammals. The opus by Ellerman and Morrison-Scott (1951) was utilized for palaearctic mammals, as were the volumes by Ellerman (1940, 1941, and 1949) in some other instances. The scheme of classification followed is essentially that of Simpson (1945) and that of Anderson and Jones (1967), but with modification for the classification of higher taxa of New World mammals as per Hershkovitz (1966, 1969). In instances where there was a conflict in generic names, Walker et al. (1964) was followed, because he generally was the latest reviser. A complete list of relevant host names is appended.

My thanks are extended to all of these associates for their cheerful and cheering help.

REFERENCES

Anderson, S. & Knox Jones, J., Jr., ed. 1967. *Recent mammals of the world. A synopsis of families.* 453 pp., New York.

Barnes, A. M. & Radovsky, F. J. 1969. A new *Tunga* (Siphonaptera) from the Nearctic Region with description of all stages. *J. med. Ent.* **6** : 19–36, illus., refs.

Costa Lima, A. da & Hathaway, C. R. 1946. *Pulgas.* 522 pp., Rio de Janeiro.

Ellerman, J. R. 1940. *The families and genera of living rodents.* Vol. I. 689 pp., London.

—— 1941. *The families and genera of living rodents.* Vol. II. 690 pp., London.

—— 1949. *The families and genera of living rodents.* Vol. III. 210 pp., London.

Ellerman, J. R. & Morrison-Scott, T. C. S. 1951. *Checklist of Palaearctic and Indian mammals. 1758 to 1946.* 810 pp., London.

Goncharov, A. I. 1964a. On the study of functions of modified segments and some parts of aedeagus important in flea diagnosis. *Trudy armyansk. Protivoch. Stn.* **3** : 437–457.

—— 1964b. On coupling (linkage) of male sternite IX of flea with aedeagus. *Trudy armyansk. Protivoch. Stn.* **3** : 459–471.

Harrison, J. L. 1964. *An introduction to the mammals of Sabah.* x + 244 pp., Singapore.

—— 1966. *An introduction to mammals of Singapore and Malaya.* Malay. Nat. Soc. (Singapore Branch), 340 pp.

Hershkovitz, P. 1966. Mice, land bridges and Latin American faunal interchange. pp. 725–751. *In* Wenzel, R. L. & Tipton, V. J., ed., *Ectoparasites of Panama.* 861 pp., Chicago.

—— 1969. The evolution of mammals on southern continents. VI. The recent mammals of the Neotropical Region : A zoogeographic and ecological review. *Quart. Rev. Biol.* **44** : 1–70.

Holland, G. P. 1955. Primary and secondary sexual characteristics of some Ceratophyllinae, with notes on the mechanism of copulation (Siphonaptera). *Trans. roy. ent. Soc. Lond.* **107** : 233–248, illus., refs.

—— 1969. Contribution towards a monograph of the fleas of New Guinea. *Mem. ent. Soc. Canad.* (61), 77 pp., illus., refs.

Hopkins, G. H. E. & Rothschild, M. 1966. *An illustrated catalogue of the Rothschild collection of fleas (Siphonaptera) in the British Museum.* Vol. 4, 549 pp., London.

Jordan, K. 1926. New Siphonaptera. *Novit. zool.* **33** : 385–394, illus.

—— 1933. Fleas collected by Dr Max Bartels in Java. *Novit. zool.* **38** : 352–357, illus.

Jordan, K. & Rothschild, N. C. 1922a. The Siphonaptera collected by Mr E. Jacobson on Sumatra. *Ectoparasites* **1** : 223–230, illus.

Jordan, K. & Rothschild, N. C. 1922b. On *Pygiopsylla* and the allied genera of Siphonaptera. *Ectoparasites* **1** : 231–265, illus.

Li, K.-C. & Wang, D.-C. 1958. The fleas of the genus *Stivalius* J. et R. 1922 (Siphonaptera) from China. *Acta ent. Sinica* 8 (1) : 67–75, illus., refs.

Medway, Lord. 1963. Mammals of Borneo. *J. Malay. Brch R. Asiat. Soc.* **36** (3) : 1–193.

Oudemans, A. C. 1909. *Pygiopsylla robinsoni* (Rothschild) ♂. *Notes* (XI) *Leyden Mus.* **31** : 195–200, illus.

Peus, F. 1956. Siphonaptera. pp. 122–131. *In* Tuxen, S. L., ed., *Taxonomist's glossary of genitalia in insects.* 284 pp., illus., Copenhagen.

Pollitzer, R. 1954. Plague. *WHO Monog.* Ser. No. 22, 698 pp., Geneve.

Pollitzer, R. & Meyer, K. F. 1961. The ecology of plague, pp. 433–501, 582–590. *In* May, J., ed., *Studies in disease ecology* (Vol. 2 in series *Studies in medical geography.*) 613 pp., New York.

Rothschild, N. C. 1905. Some new Siphonaptera. *Novit. zool.* **12** : 479–491, illus.

—— 1906. Some new exotic fleas. *Ent. mon. Mag.* (2) **17** : 221–224, illus.

—— 1908. New Siphonaptera. *Proc. zool. Soc. Lond.* **50** : 617–629, illus.

—— 1919. Siphonaptera collected in Korinchi, West Sumatra by Messrs H. C. Robinson and C. Boden Kloss. *J. fed. Malay St. Mus.* **8**(3) : 1–6, illus.

Schwarz, E. & Schwarz, H. K. 1965 (1967). A monograph of the *Rattus rattus* group. *An. Esc. nac. Cienc. biol., Mex.* **14** : 80–178, illus., refs.

Simpson, G. G. 1945. The principles of classification and a classification of mammals. *Bull. Am. Mus. nat. Hist.* **85**, 350 pp.

Smit, F. G. A. M. 1958. The African species of *Stivalius*, a genus of Siphonaptera. *Bull. Br. Mus.* (*Nat. Hist.*) *Ent.* **7** : 41–76, illus., refs.

Snodgrass, R. E. 1946. The skeletal anatomy of fleas (Siphonaptera). *Smithson misc. Collns.* **104**, 89 pp., illus.

Suter, P. R. 1964. Biologie von *Echidnophaga gallinacea* (Westw.) und Vergleich mit andern Verhaltenstypen bei Flöhen. *Acta trop.* **21** : 193–238, illus., refs.

Traub, R. 1950a. Siphonaptera from Central America and Mexico. A morphological study of the aedeagus with descriptions of new genera and species. *Fieldiana Zool. Mem.* **1** : 1–127, illus., refs.

—— 1950b. Notes on Indo-Malayan fleas, with descriptions of new species (Siphonaptera). *Proc. ent. Soc. Wash.* **52** : 169–143, illus., refs.

—— 1952. Fleas collected by the Chicago Natural History Museum Expedition to the Philippines, 1946–1947. *Proc. biol. Soc. Wash.* **64** : 1–21, illus., refs.

—— 1966. Some examples of convergent evolution in Siphonaptera. (Abstract of paper presented at meeting of Society, Dec. 1966: *Proc. r. ent. Soc. Lond.* (C) **31**(7) : 37–38.) Reported in *Ibid.* **31** : 46–47 (1966–1967) with errata in *Ibid.* **31** : 79 (1966–1967).

—— 1969. *Muesebeckella*, a new genus of flea from New Guinea (Siphonaptera, Pygiopsyllidae). *Proc. ent. Soc. Wash.* **71** : 374–396, illus., refs.

Walker, E. P., Warnich, F., *et al.*, 1968. *Mammals of the world.* Vols. I–II : 1–646, 647–1500, Baltimore.

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LIST OF HOST-NAMES[19]

Apodemus speciosus Temminck, 1845
Apomys Mearns, 1905
Callosciurus Gray, 1867
Callosciurus caniceps (Gray, 1842)
Callosciurus erythraeus (Pallas, 1779)
Callosciurus finlaysoni (Horsfield, 1824)
Callosciurus n. nigrovittatus (Horsfield, 1824)
Callosciurus notatus (Boddaert, 1785)
Callosciurus notatus miniatus (Miller, 1900)
Callosciurus prevosti (Desmarest, 1822)
Dremomys Heude, 1898
Dremomys rufigenis (Blanford, 1878)
Epimys rattus (Linnaeus, 1758)
Hylopetes Thomas, 1908
Iomys horsfieldi (Waterhouse, 1837)
Lariscus Thomas & Wroughton, 1909
Lariscus insignis (Cuvier, 1821)
Menetes berdmorei (Blyth, 1849)
Millardia Thomas, 1911
Petaurista Link, 1795
Petaurista elegans (Müller, 1839)
Ptilocercus lowi (Gray, 1848)
Rattus Fischer, 1803
Rattus (*Lenothrix*) *canus* (Miller, 1903)
Rattus (*Lenothrix*) *rajah* (Thomas, 1894)
Rattus (*Lenothrix*) *surifer* (Miller, 1900)
Rattus (*Leopoldamys*) *sabanus* (Thomas, 1887)
Rattus (*Maxomys*) *cremoriventer* (Miller, 1900)
?*Rattus* (*Maxomys*) *fulvescens temmincki* Kloss, 1921 (for "Rattus bukit temmincki")
Rattus (*Rattus*) Fischer, 1803
Rattus (*Rattus*) *concolor* (Blyth, 1859)
Rattus (*Rattus*) *querceti* Hollister, 1911
Rattus (*Rattus*) *rattus* (Linnaeus, 1758)
Rattus (*Rattus*) *rattus mindanensis* (Mearns, 1905)
Rattus (*Rattus*) *rattus negrinus* Thomas, 1898
Rattus (*Rattus*) *tiomanicus* (Miller, 1900)
Rattus (*Rattus*) *tiomanicus jalorensis* (Bonhote, 1903)
Rattus (*Stenomys*) *bowersi* (Anderson, 1879)
Rattus (*Stenomys*) *muelleri* (Jentink, 1879)
Ratufa Gray, 1867
Rhinosciurus Blyth, 1855
Rhinosciurus laticaudatus (Müller, 1844)
Sundasciurus Moore, 1958
Sundasciurus brookei (Thomas, 1892)
Sundasciurus hippurus (Geoffroy, 1832)
Sundasciurus lowi (Thomas, 1892)
Sundasciurus tenuis (Horsfield, 1824)
Tamiops mcclellandi (Horsfield, 1839)
Tupaia Raffles, 1821
Tupaia glis (Diard, 1820)
Tupaia javanica Horsfield, 1822
Tupaia javanica occidentalis Robinson & Kloss, 1918
Tupaia minor Günther, 1876
Tupaia tana Raffles, 1821

LIST OF LANDMARKS AND POINTS OF REFERENCE

(Figs 1–3, 28 and 29)

FIG. 1

a Anteroventral angle of tergal apodeme of ♂ segment 9 (T.AP.9).
b Ventral sinus of T.AP.9.
c Anterodorsal angle of T.AP.9.
d Dorsal sinus of T.AP.9 and base of anterior margin of conical process (C.P.).
e Apex of C.P.
f Level of middle of C.P.; anterior margin.
g Level of middle of C.P.; posterior margin.
h Middle of base of C.P.
i Point of maximum convexity on anterior margin of movable finger (F.).
j Level of narrowest subapical portion of F.; anterior margin.
k Level of narrowest subapical portion of F.; posterior margin.
l Level for measuring length of dilated portion of apex of F.; anterior margin.
m Apicodorsal angle of F.
n Midpoint of apical margin of F.; for measuring height of F.
o Level of base of stiva (STV.); a projection of posterior margin of F. at narrowest level (k).

[19] Not all of these names are necessarily regarded by mammalogists as valid today.

p Apex of stiva.
q Point of maximum convexity on posterior margin of F.
r Level of most apical portion of immovable process of clasper (P.).
s Level of r, projected to longitudinal axis of F.
t Level of base of bulge at apex of P.
u Point of maximum convexity on upper or dorsal bulge on posterior margin of manubrium (MB.).
v Point of maximum concavity on sinus on posterior margin of MB.
w Point of maximum convexity on lower or apical bulge of MB.
x Base of apical cap of MB. (posterior margin).
y Tip of apical cap of MB.
z Base of apical cap of MB. (anterior margin).
aa Apex of anterior (ventral) margin of proximal arm of sternum 9 (P.A.9).
bb Apex of posterior (dorsal) margin of P.A.9.
cc Subapical bulge (convexity) on anterior margin of P.A.9.
dd Posterior or ventral bulge on anterior margin of P.A.9.
ee Point on posterior margin of P.A.9 that is opposite cc (paralleling chord on arc aa–bb).
ff Point on posterior margin of P.A.9 that is opposite dd.
gg Lowest point on trough or "U" on dorsal margin at base of P.A. 9.
hh Point on ventral margin of P.A.9 opposite gg.
ii Base of distal arm of sternum 9 (D.A.9); anterior margin.
jj Anterior (dorsal) end of transverse sclerotization (T.S.) of D.A.9 and level of base of ventral (caudal) margin of mid-microspiculate area (M.MSP.).
kk Base of sclerotized part of apical half of D.A.9; distad of mid-microspiculate area (M.MSP.) and level of proximal-most of caudomedial group of spiniform bristles (CM.G.B.) (see also fig. 3).
ll Proximal marginal point of base of subapical lobe (SUB.L.), at level of proximal-most bristle of SUB.L.
mm Apex of SUB.L. (see also fig. 3).
nn Midpoint of imaginary chord connecting edge of subapical notch (NCH.).
oo Apicoventral angle of apical lobe AP.L. of D.A.9.
pp Midpoint on margin of AP.L.
qq Apicodorsal angle (or point in line with oo) on AP.L. (see also fig. 3).
rr Lowest point in subapical notch (NCH.) on D.A.9.
ss Level of distalmost member of subapical group of spiniforms (SG.SPN.).
tt Level of proximal-most of CM.G.B.
uu Posterior (ventral) margin of T.S.
vv Base of D.A.9 (posterior margin).
ww Anteroventral angle of upper margin of fulcral sclerite (F.S.).
xx Caudodorsal angle of upper margin of fulcral sclerite (F.C.)
yy Dorsal extension of F.S. curving to ventrocaudal angle of F.
zz Anteroventral angle of lower or ventrocaudal margin of F.S.
a3 Upper angle of ventrocaudal margin of F.S., opposite zz.

FIG. 3

b3 Dorsal point of transverse sclerotization (T.S.) of D.A.9 in *M. loncha* and allies (but not ventral margin of M.MSP.).
c3 Ventral or proximal base of spur-like subapical lobe (SUB.L.) of D.A.9 in *M. loncha* and allies.
d3 Thickening at base of SUB.L.
e3 Dorsal or apical base of SUB.L.
f3 Semimembranous margin of D.A.9 distad of e3.
g3 Level of base of spinform opposite d3 at base of SUB.L.

FIGS 28, 29

h3 Dorsal margin of 8 S.—projection of upper portion (anterior fork) of SU.8.
i3 Dorsalmost point of 8 S.
j3 Dorsal margin—in line with middle of dorsal margin (o3) of LUM. and dorsalmost median large bristle (k3).
k3 Dorsalmost large median bristle (in line with middle of LUM.).
l3 Point on anterior margin, near middle, in line with largest caudomarginal bristle (m3).
m3 Longest and secondmost dorsal, caudomarginal bristle.
n3 Anteriormost point on tanned dorsal margin of LUM.
o3 Middle of LUM. as located on dorsal margin.
p3 Ventrocephalad corner of 8 S.
q3 Anteriormost point on ventral margin of LUM. indicated by limit of dense group of rows of spiniforms.
r3 Point on ventral margin directly below highest point (i3).
s3 Caudal apex of LUM.
t3 Ventrocaudal corner of 8 S.

FIG. 3

u3 Projection of axis of T.S. to ventral margin of D.A.9.

FIG. 2

v3 Level of dorsal margin of head at falx.
w3 Falx.
x3 Point along antennal fossa in line with bottom of median sensory crater (M.S.C.).
y3 Point along frons in line with x3.
z3 Point along frons in line with base of uppermost bristle of row I.
a4 Point along antennal fossa in line with z3.
b4 Point along frons in line with base of uppermost bristle of row II.
c4 Point along antennal fossa in line with labral bristles (d4) and base of eye-bristle (E.B.).
d4 Level of labral bristles.
e4 Point along antennal fossa in line with labral bristles and E.B.
f4 Point on ventral margin of gena in line with w3 (falx) and height of convexity of first ventral arc of gena.
g4 Point of height of convexity of second ventral arc of gena.

LIST OF ABBREVIATIONS

A.B.	Antepygidial bristles.	ARC.	Broad sinus or arc on D.A. 9.
A.G.	Apical group of dorsomarginal bristles on tibia.	B.	Bulga (head) of spermatheca.
A.LB.9	Short apical lobe on D.A.9.	B.C.	Bursa copulatrix.
A.S.	Anal stylet.	B.CR.	Body of crochet.
AC.F.9	Apicocaudal flap of D.A.9.	B.M.L.	Bay of middle lamina.
AE.A.	Aedeagal apodeme.	B.MB.	Bay of manubrium.
AE.F.	Aedeagal fulcrum.	C.P.	Conical process on anterior portion of P.
AE.P.	Aedeagal ponch.	C.S.	Crescent sclerite of aedeagus.
AE.P.-L.	Lateral walls of AE.P.	CAV.SPIC.	Caverna spiculosa.
AE.P.-V.	Thickened ventral walls of AE.P.	CEN.S.	Central sclerite of aedeagus.
ALPH.	Alpha-portion of Ford's sclerite.	CM.G.B.	Caudomarginal group of stout bristles on D.A.9.
AN.GP.	Anterior group of marginal bristles on F.	COX.1	Procoxa.
AP.L.	Apical lobe of D.A.9.	COX.3	Metacoxa.
AP.R.	Third apodemal rod of endophallus.	CR.P.	Crochet process.
		D.A.L.	Dorsal anal lobe of proctiger.

D.A.9	Distal arm of male sternum 9.
D.B.C.	Duct of bursa copulatrix.
D.FR.	Distal fringe of long bristles on caudal margin of F.
D.S.C.	Dorsal sensillary crater of preantennal region.
D.SP.	Duct of spermatheca.
D.V.	Dorsal virga.
D.VG.	Duplicatura vaginalis.
DEL.FL.	Deltoid flap of hood of aedeagus.
DIL.P.	Dilated portion of duct of spermatheca.
DM.1–6	Groups of dorsolateral bristles arising from marginal notches on tibia.
E.B.	Large bristle in front of or near eye.
E.R.B.	Eye-row of bristles.
EXT.9	Spur-like extension of ventral apical margin of D.A.9.
F.	Movable finger or process of clasper.
F.S.	Fulcral sclerite at base of attachment of F.
F.SC.	Ford's sclerite.
FIS.	Fistula.
FM.1	Profemur.
FRK.	Freak—grossly abnormal bristle.
FUL.L.L.	Fulcral lateral lobes of aedeagus.
FUL.M.L.	Fulcral medial lobe of aedeagus.
G.	Girdle of aedeagal pouch.
G.R.B.	Genal row of bristles.
G.VG.	Glandula vaginalis.
GRV.	Groove-like structure of Ford's sclerite.
H.	Hilla (tail) of spermatheca.
HD.	Hood of aedeagus.
HOM.	Homolate margin proximad of apex of D.A.9.
L.A.	Lower arm of securifer.
L.L.	Lateral lobe of aedeagus.
L.L.7	Lower lobe of tergum 7, below plate of antepygidial bristles.
L.LAM.	Lateral laminae of aedeagal apodeme.
L.M.	Lateral metanotal area of metathorax.
L.M.B.	Lower modified bristle(s) of 7 T.
L.M.B.-2	Second or ventral L.M.B.
L.P.	Labial palpus.
L.S.C.	Lateral shafts of capsule of aedeagus.
L.W.AR.	Lateral wings of ventral armature of S.I.T.
LUM.	Lumacaudate process.
M.D.L.	Median dorsal lobe of aedeagus.
M.LAM.	Middle lamina of aedeagal apodeme.
M.MSP.	Mid-microspiculate area of D.A.9.
M.P.	Maxillary palpus.
M.R.8	Mesal tanned genitalic ridge of ♀ 8 T.
M.S.C.	Median sensillary crater of preantennal region.
MB.	Manubrium.
MPM.	Mesepimere.
MPS.	Mesepisternum.
MSN.	Mesonotum.
MSP.P.	Patch of microspicules near apex of D.A.9.
MTM.	Metepimere.
MTN.	Metanotum.
MTS.	Metepisternum.
MX.	Maxillary lobe.
NCH.	Subapical notch on anterior margin of D.A.9.
OV.	Oviduct.
P.	Immovable process of clasper.
P.A.9	Proximal arm of ♂ sternum 9.
P.B.C.	Perula—dilated portion of bursa copulatrix.
P.R.	Penis rods.
P.W.EX.	Extension of aedeagal pouch wall.
PAP.	Apical papilla on bulga.
PG.M.	Paragenital morion.
PHY.	Phylax.
PIV.CD.	Pivotal chord linking phylax and Ford's sclerite.
PIV.R.	Pivotal ridge of phylax.
PK.	Peak of bulga.
PL.A.	Pleural arch of metathorax.
PS.S.	Pseudosetae.
Q.C.	Quasi-crochet.
S.G.	Group of sensilla near anterodistal angle of F.
S.G.SPN.	Subapical group of short spiniforms on caudal margin of D.A.9.
S.I.T.	Sclerotized inner tube of aedeagus.
S.LUM.	Apical fold or seam of LUM.
S.S.	Subanal sclerite of male.
SAC.	Large sac associated with perula.
SAT.S.	Satellite sclerite of aedeagus.
SEC.	Securifer—ventrocaudal or apical member of Ford's sclerite.
SN.	Sensilium.

SP.	Spermatheca.
SPIC.L.	Ventral lamella or semimembranous spiculose lobe arising from base of PHY.
SQ.	Squamulum.
STV.	Stiva—caudodistal expansion of F., resembling a plow-handle in shape.
SU.8.	Suture delimiting more heavily sclerotized mesal area of ♂ 8 S.
SUB.L.	Subapical lobe on anterior margin of D.A.9.
SUP.FL.	Supramedial flap of D.A.9.
SUP.G.	Supramedial group of thin bristles on D.A.9.
SY.	"Supernumerary" bristles between rows on head.
T.AP.9	Tergal apodeme of segment 9.
T.L.S.	Tendons of lateral shafts of aedeagus.
T.S.	Transverse submedian sclerotization of D.A.9.
THK.	Sclerotized thickening associated with SUP.FL.
THM.	Thumb-like apex of alpha-portion of F.SC.
U.A.	Upper arm of securifer.
U.L.7	Upper lobe of tergum 7, above plate of antepygidial bristles.
U.M.B.	Upper modified bristle of 7 T.
V.	Vesicle of aedeagus.
V.A.L.	Ventral anal lobe of proctiger.
V.S.C.	Ventral sensillary crater of preantennal region.
V.V.	Ventral virga.
VAG.	Vagina.
VC.1–4	Vinculum 1–4.
Y.S.	Y-sclerite of aedeagus.
1 T.	First tergum.
2 S.	Second sternum
2 T.	Second tergum.
6 S.	Sixth sternum.
6 T.	Sixth tergum.
7 S.	Seventh sternum.
7 SPC.	Spiracle (fossa) of seventh segment.
7 T.	Seventh tergum.
8 S.	Eighth sternum.
8 SPC.	Spiracle (fossa) of eighth segment.
8 T.	Eighth tergum.
9 S.	Ninth sternum.

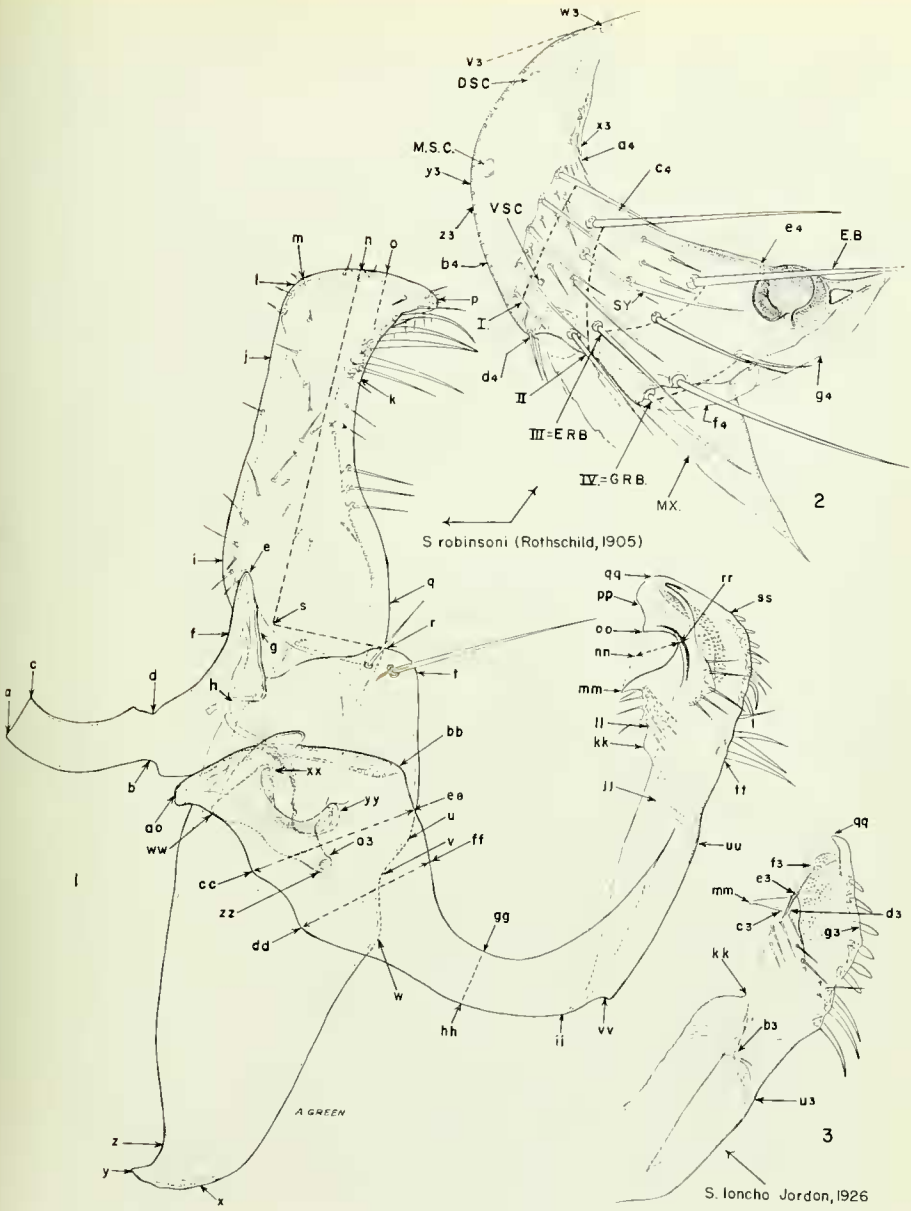
LIST OF ILLUSTRATIONS

Fig.		
1.	Clasper and sternum 9	*Medwayella r. robinsoni* (Roths., 1905)
2.	Preantennal region (♂)	,, ,, ,,
3.	Distal arm of sternum 9	,, *loncha* (Jordan, 1926)
4.	Head and prothorax (♂)	,, *dryadosa* sp. nov.
5.	Lateral metanotal area (♂)	,, ,,
6.	Head (♀)	,, ,,
7.	Apical segments of protarsus	,, ,,
8.	Segment 5 of ♂ metatarsus	,, ,,
9.	Meso- and metathorax	,, ,,
10.	Aedeagus	,, ,,
11.	Modified abdominal segments (♂)	,, ,,
12.	Lumacaudate process	,, ,,
13.	Dorsal and ventral anal lobes (♂)	,, ,,
14.	Processes of clasper	,, ,,
15.	Spermatheca	,, ,,
16.	Anal lobes and stylet (♀)	,, ,,
17.	Processes of clasper	,, *r. robinsoni*
18.	Clasper and sternum 9	,, *dryadosa* sp. nov.
19.	Metatibia (♂)	,, ,,
20.	Distal arm of sternum 9	,, ,,
21.	Distal arm of sternum 9	,, *r. robinsoni*
22.	Apical region of aedeagus (lateral aspect)	,, *dryadosa* sp. nov.
23.	Apical region of aedeagus	,, *r. robinsoni*
24.	Apex of aedeagus (dorsal aspect)	,, *dryadosa* sp. nov.

25.	Apex of aedeagus (ventral aspect)	,,	,,
26.	Modified abdominal segments (♀)	,,	,,
27.	Spermatheca, genitalia and anal segments	,,	,,
28.	Sternum 8 (♂)	,,	*r. robinsoni*
29.	Sternum 8 (♂)	,,	*dryadosa* sp. nov.
30.	Segment 7 (♀)	,,	,,
31.	Genitalia (♀)	,,	,,
32.	Genitalia (♀)	,,	*r. robinsoni*
33.	Distal arm of sternum 9	,,	*arcuata* sp. nov.
34.	Processes of clasper	,,	,,
35.	Processes of clasper	,,	*angustata* sp. nov.
36.	Distal arm of sternum 9	,,	,,
37.	Modified abdominal segments (♀)	,,	,,
38.	Spermatheca, genitalia and anal segments	,,	,,
39.	Lumacaudate process	,,	,,
40.	Genitalia (♀)	,,	*javana* (Jordan, 1933)
41.	Genitalia (♀)	,,	*angustata* sp. nov.
42.	Apex of aedeagus	,,	*dryadosa* sp. nov.
43.	Sclerotized inner tube	,,	,,
44.	Apex of aedeagus	,,	*r. robinsoni*
45.	Apex of aedeagus	,,	*angustata* sp. nov.
46.	Apical region of aedeagus	,,	*r. robinsoni*
47.	Clasper and sternum 9	,,	,,
48.	Transverse suture, D.A.9	,,	,,
49.	Sternum 7 (♀)	,,	,,
50.	Lateral metanotal area (♂)	,,	,,
51.	Anal segments (♀)	,,	,,
52.	Spermatheca	,,	,,
53.	Distal arm of sternum 9	,,	*r. tiomanica* subsp. nov.
54.	Distal arm of sternum 9	,,	*r. bogora* subsp. nov.
55.	Distal arm of sternum 9	,,	*r. peregrinata* subsp. nov.
56.	Apex of aedeagus	,,	*r. tiomanica* subsp. nov.
57.	Apex of aedeagus	,,	*r. peregrinata* subsp. nov.
58.	Apex of aedeagus	,,	*r. bogora* subsp. nov.
59.	Genitalia and anal lobes (♀)	,,	*r. robinsoni*
60.	Spermatheca and sternum 7	,,	*r. peregrinata* subsp. nov.
61.	Genitalia (♀)	,,	,,
62.	Spermatheca, genitalia and sternum 7	,,	*r. bogora* subsp. nov.
63.	Proximal arm of sternum 9	,,	,,
64.	Spermatheca, genitalia and sternum 7	,,	*r. tiomanica* subsp. nov.
65.	Processes of clasper	,,	*phangi tana* subsp. nov.
66.	Processes of clasper	,,	*phangi phangi* sp. nov.
67.	Distal arm of sternum 9	,,	*p. tana* subsp. nov.
68.	Distal arm of sternum 9	,,	*p. phangi* sp. nov.
69.	Sternum 8 (♂)	,,	,,
70.	Lumacaudate process	,,	,,
71.	Apical region of aedeagus	,,	,,
72.	Tergum 8 (♀)	,,	,,
73.	Anal lobes and stylet (♀)	,,	,,
74.	Spermatheca	,,	,,
75.	Sternum 7 (♀)	,,	*p. tana* subsp. nov.
76.	Sternum 7 (♀)	,,	*p. phangi* sp. nov.
77.	Spermatheca, genitalia and anal segments	,,	,,
78.	Spermatheca (variation in aspect)	,,	*limi* sp. nov.

79.	Spermatheca and genitalia	,,	,,
80.	Processes of clasper	,,	,,
81.	Distal arm of sternum 9	,,	,,
82.	Apex of aedeagus	,,	,,
83.	Lumacaudate process	,,	,,
84.	Spermatheca and genitalia	,,	,,
85.	Sterna 8 and 9 (♀)	,,	,,
86.	Head and prothorax (♂)	,,	*thurmani* sp. nov.
87.	Movable finger	,,	,,
88.	Spermatheca	,,	,,
89.	Sensilium and anal segments (♀)	,,	,,
90.	Apical region of aedeagus	,,	,,
91.	Distal arm of sternum 9	,,	,,
92.	Processes of clasper	,,	,,
93.	Apical region of aedeagus	,,	*dryadosa* sp. nov.
94.	Apex of aedeagus	,,	*thurmani* sp. nov.
95.	Apex of aedeagus	,,	*javana*
96.	Sclerotized inner tube	,,	,,
97.	Apical region of aedeagus	,,	*thurmani* sp. nov.
98.	Apical region of aedeagus	,,	*arcuata* sp. nov.
99.	Sternum 7 (♀)	,,	*thurmani* sp. nov.
100.	Lateral metanotal area (♂)	,,	,,
101.	Sternum 8 (♂)	,,	,,
102.	Spermatheca and genitalia	,,	,,
103.	Spermatheca, genitalia and anal segments	,,	*calcarata* sp. nov.
104.	Head and prothorax (♂)	,,	,,
105.	Lateral metanotal area (♂)	,,	,,
106.	Lateral metanotal area (♂)	,,	*batibacula* sp. nov.
107.	Lumacaudate process	,,	*calcarata* sp. nov.
108.	Processes of clasper	,,	,,
109.	Processes of clasper	,,	*batibacula* sp. nov.
110.	Mesal aspect of F.	,,	,,
111.	Distal arm of sternum 9	,,	*calcarata* sp. nov.
112.	Distal arm of sternum 9	,,	*batibacula* sp. nov.
113.	Apex of aedeagus	,,	*calcarata* sp. nov.
114.	Apex of aedeagus	,,	*veruta* sp. nov.
115.	Apex of aedeagus	,,	*batibacula* sp. nov.
116.	Lumacaudate process	,,	,,
117.	Spermatheca and genitalia	,,	*veruta* sp. nov.
118.	Spermatheca and genitalia	,,	*loncha*
119.	Processes of clasper	,,	*veruta* sp. nov.
120.	Distal arm of sternum 9	,,	,,
121.	Sternum 8 (♂)	,,	,,
122.	Anal lobes and stylet (♀)	,,	,,
123.	Spermatheca	,,	,,
124.	Sternum 7 (♀)	,,	,,
125.	Genitalia (♀)	,,	,,
126.	Processes of clasper	,,	*loncha*
127.	Distal arm of sternum 9	,,	,,
128.	Apex of aedeagus	,,	,,
129.	Sensilium and anal segments (♀)	,,	,,
130.	Sternum 7 (♀)	,,	,,
131.	Sternum 8 (♂)	,,	,,
132.	Spermatheca	,,	,,

133.	Processes of clasper	,, *javana*
134.	Distal arm of sternum 9	,, ,,
135.	Lumacaudate process	,, ,,
136.	Sternum 7 (♀)	,, ,,
137.	Spermatheca, genitalia and anal segments	,, ,,
138.	Modified abdominal segments (♂)	,, *rhaeba* (Jordan, 1926)
139.	Modified abdominal segments (♀)	,, ,,
140.	Head and prothorax (♂)	*Lentistivalius vomerus* sp. nov.
141.	Head (♀)	,, ,,
142.	Meso- and metathorax (♂)	,, ,,
143.	Clasper and segment 9	,, ,,
144.	Distal arm of sternum 9	,, ,,
145.	Distal arm of sternum 9	,, *insolli* (Traub, 1950)
146.	Clasper and segment 9	,, ,,
147.	Modified abdominal segments (♂)	,, *vomerus* sp. nov.
148.	Aedeagus	,, ,,
149.	Metatibia (♂)	,, ,,
150.	Segment 5 of metatarsus (♂)	,, ,,
151.	Metatibia (♀)	,, ,,
152.	Apical region of aedeagus (lateral)	,, ,,
153.	Apical region of aedeagus (ventral)	,, ,,
154.	Apical region of aedeagus (lateral)	,, *insolli*
155.	Apical region of aedeagus (lateral)	,, *aestivalis* (Jameson & Sakaguti, 1954)
156.	Modified abdominal segments (♀)	,, *vomerus* sp. nov.
157.	Anal segments and stylet (♀)	,, ,,
158.	Spermatheca	,, ,,
159.	Abdominal segments 2 (♀)	,, ,,
160.	Spermatheca and genitalia	,, ,,
161.	Spermatheca (variation)	,, ,,
162.	Bursa copulatrix	*Stivalius phoberus* J. & R., 1922
163.	Spermatheca and genitalia	,, *cognatus bamus* subsp. nov.
164.	Head and prothorax (♂)	,, ,, ,,
165.	Processes of clasper	,, ,, ,,
166.	Antepygidial region (♀)	,, ,, ,,
167.	Distal arm of sternum 9	,, ,, ,,
168.	Distal arm of sternum 9	,, *c. cognatus* J. & R., 1922
169.	Distal arm of sternum 9	,, *c. spiramus* Jordan, 1926
170.	Apical region of aedeagus (lateral)	,, *c. bamus* subsp. nov.
171.	Apical region of aedeagus (ventral)	,, ,,
172.	Apical region of aedeagus	*Lentistivalius vomerus* sp. nov.
173.	Apical region of aedeagus	*Stivalius c. spiramus*
174.	Apical region of aedeagus	,, *c. bamus* subsp. nov.
175.	Sternum 7 (♀)	,, *c. spiramus*
176.	Spermatheca, genitalia and anal segments	,, *c. bamus* subsp. nov.
177.	Spermatheca and bursa copulatrix	,, ,,
178.	Bursa copulatrix	,, *c. spiramus*
179.	Spermatheca and bursa copulatrix	,, *c. cognatus*


w3
v3
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VSC
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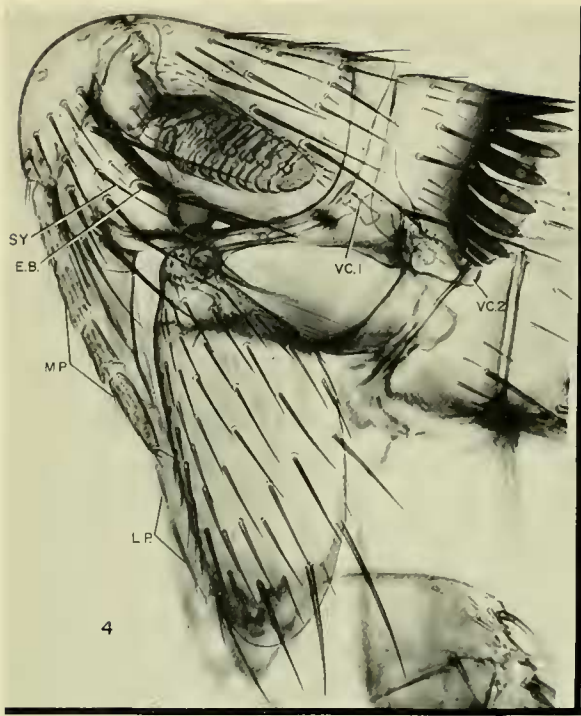
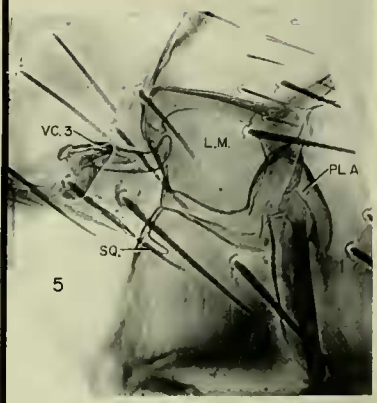
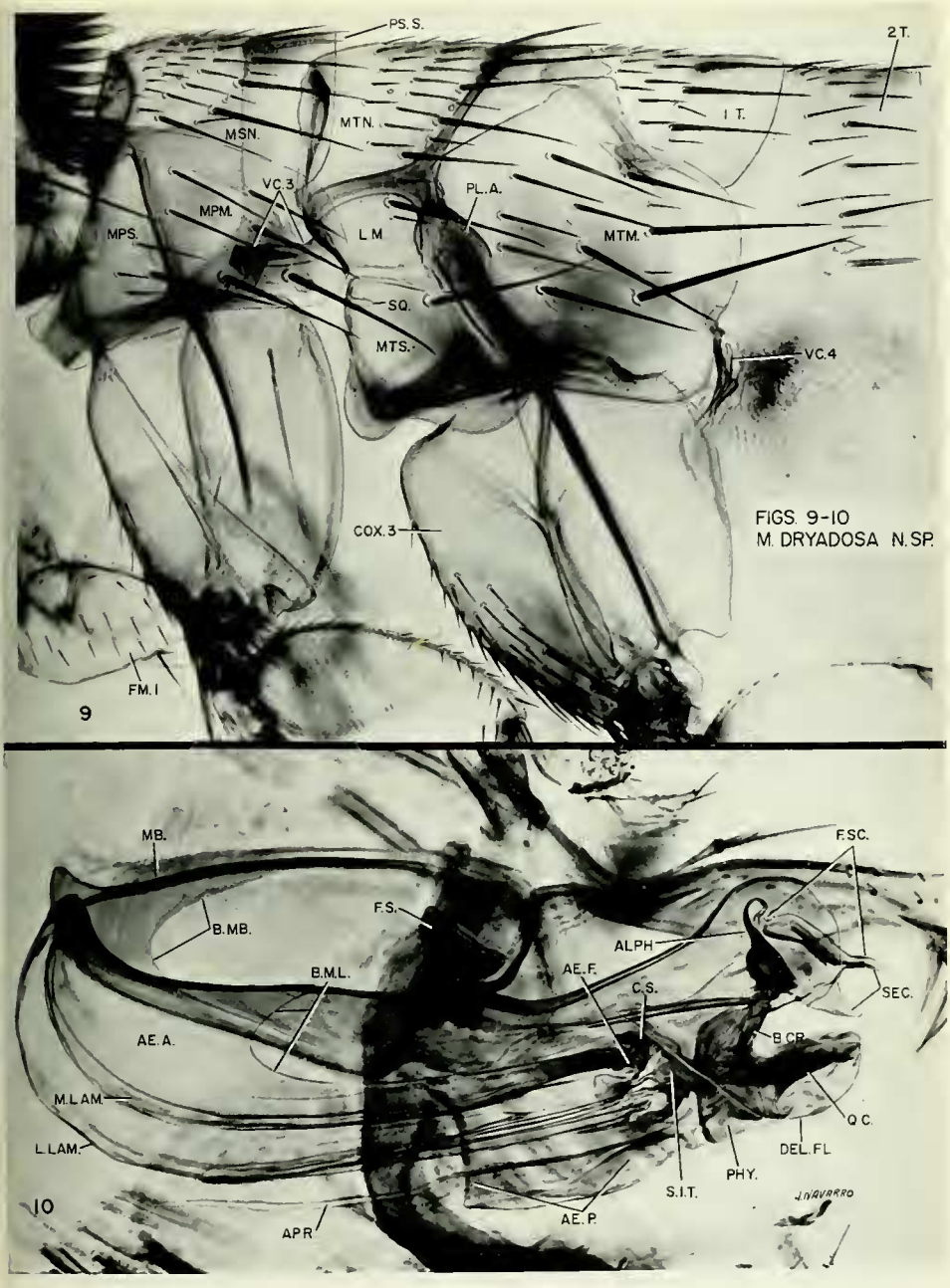
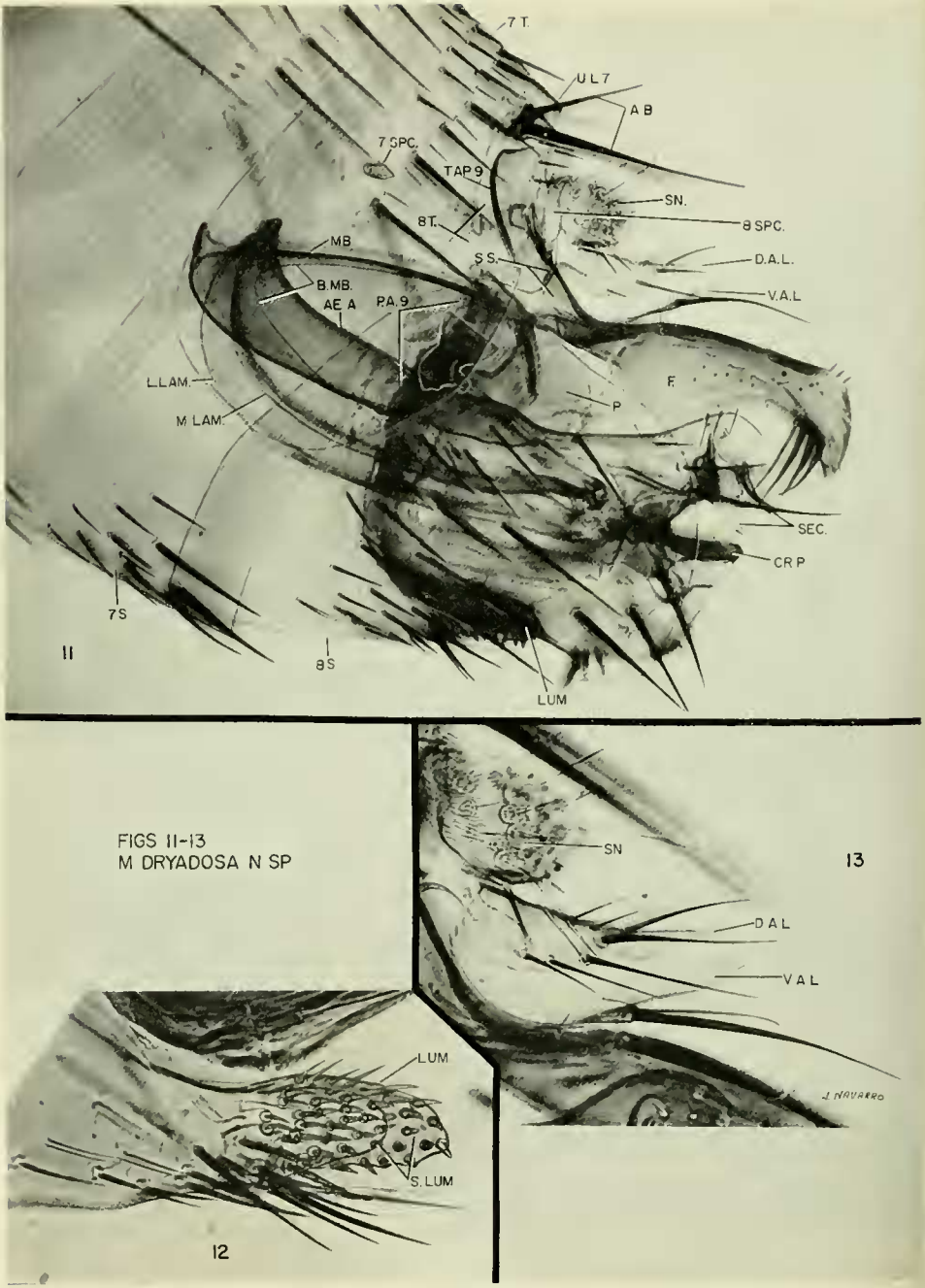
III=ERB
IV=GRB.
MX.
f4
g4
2
S robinsoni (Rothschild, 1905)
m
n
o
l
p
j
k
i
e
q
s
f
g
r
t
h
c
d
a
b
bb
xx
yy
ee
u
ao
ww
o3
v
ff
cc
zz
dd
gg
w
hh
ii
vv
1
qq
rr
pp
ss
oo
nn
mm
ll
kk
jj
tt
uu
A GREEN
z
y
x
qq
f3
e3
mm
d3
c3
g3
kk
b3
u3
3
S. loncho Jordon, 1926

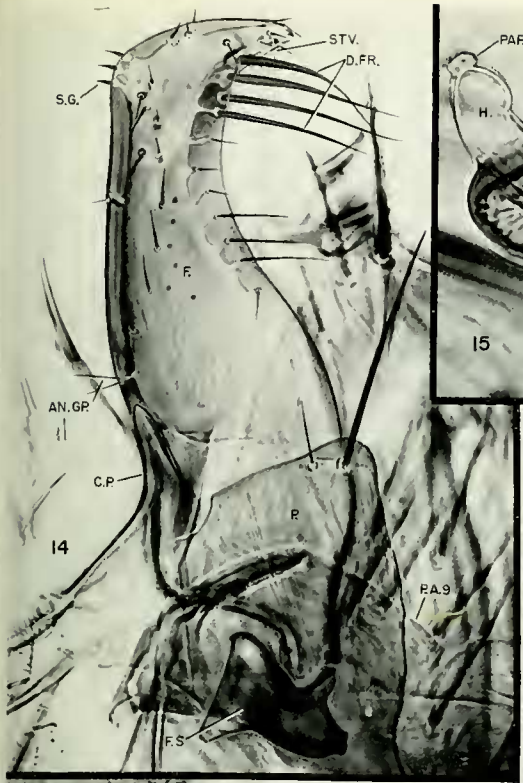


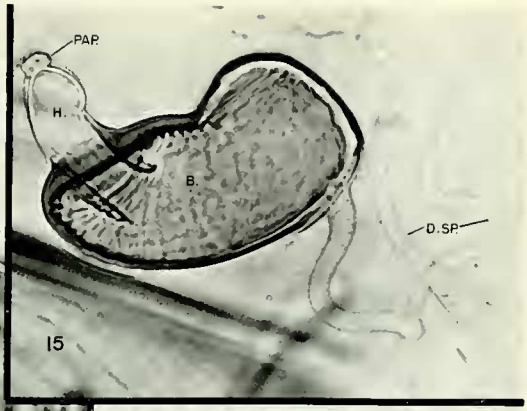


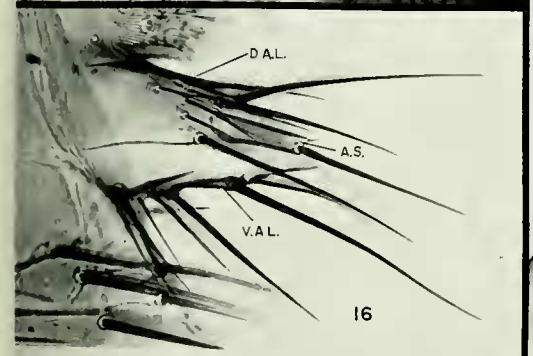
FIGS 4-8
M. DRYADOSA N SP


PS.S.
2T.
MSN.
MTN.
I.T.
VC.3
PL.A.
MPM.
MPS.
L.M.
MTM.
SQ.
MTS.
VC.4
COX.3
FIGS. 9-10
M. DRYADOSA N.SP.
FM.I
9
MB.
F.SC.
F.S.
B.MB.
ALPH
B.M.L.
AE.F.
C.S.
SEC.
AE.A.
B.CR.
M.L.AM.
Q.C.
L.LAM.
DEL.FL
PHY.
S.I.T.
10
APR
AE.P.
J.NAVARRO


7 T.
U L 7
A B
7 SPC.
TAP 9
SN.
8 T.
8 SPC.
MB.
S S.
D.A.L.
B.MB.
AE A
PA.9
V.A.L
L.LAM.
M. LAM.
F.
P
SEC.
CR P
7S
11
8S
LUM
FIGS 11-13
M DRYADOSA N SP
SN
13
D A L
V A L
J. NAVARRO
LUM
S. LUM
12







FIGS. 14-16
M DRYADOSA N SP.

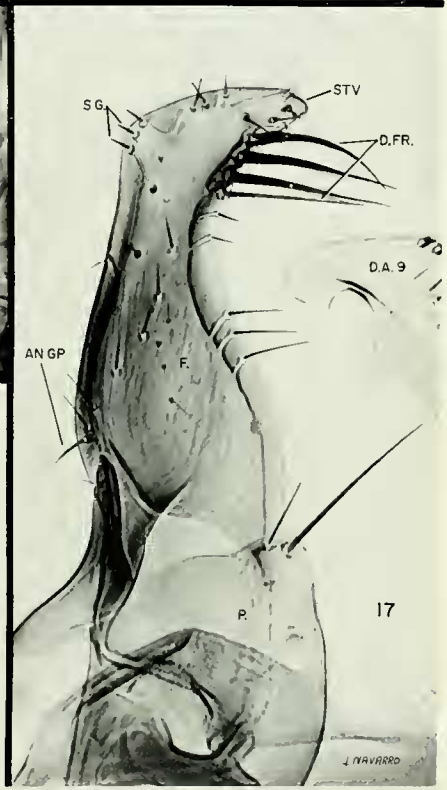
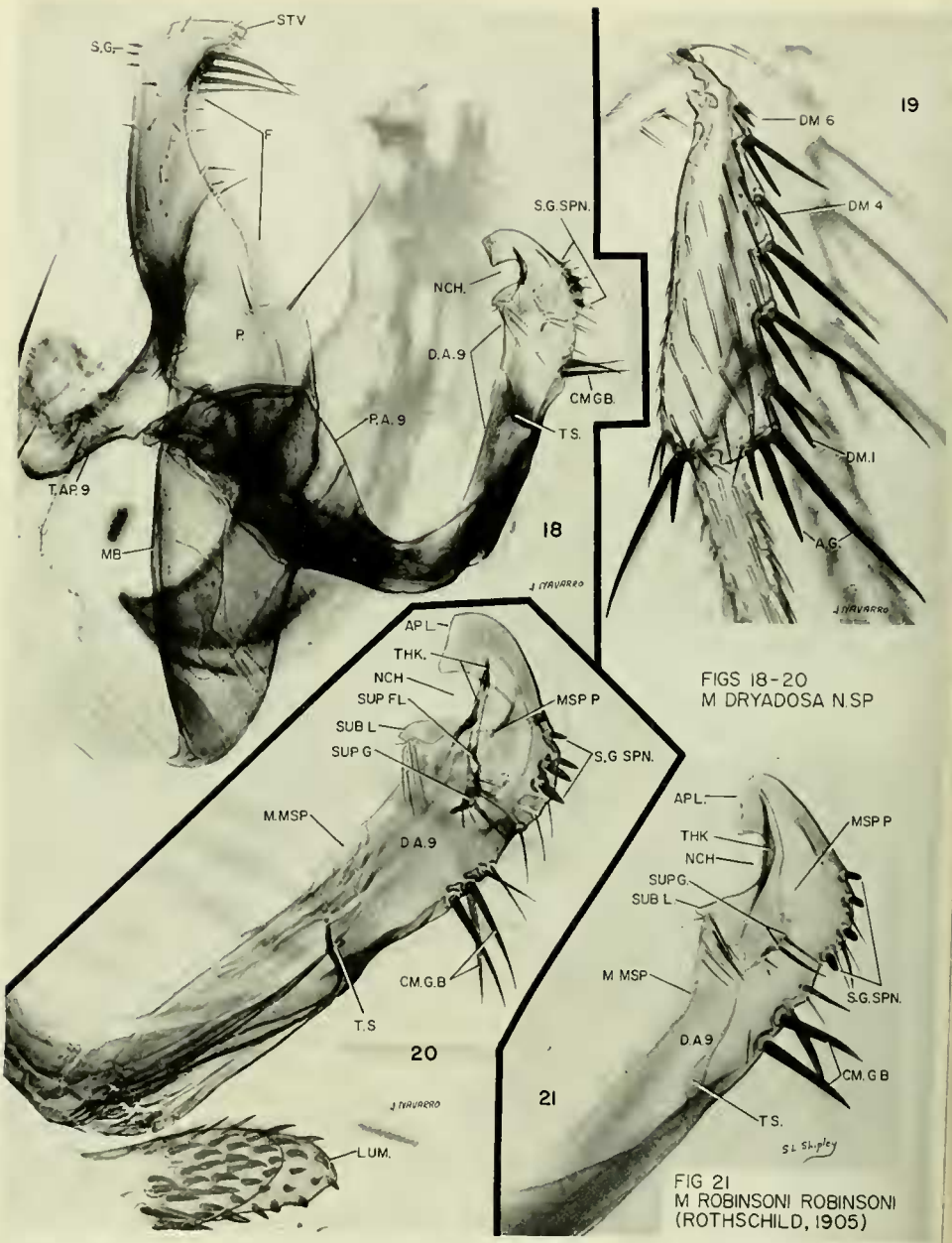
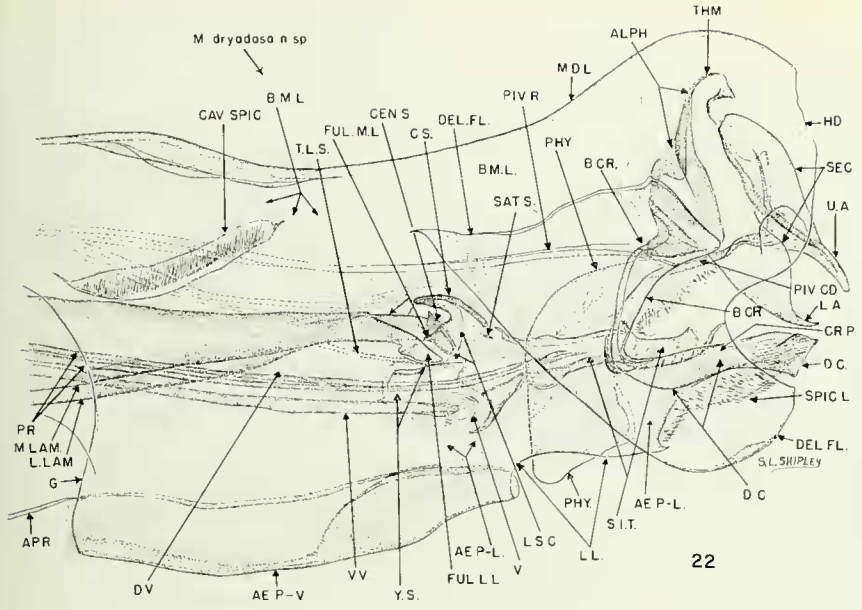


FIG. 17
M ROBINSONI ROBINSONI
(ROTHSCHILD, 1905)

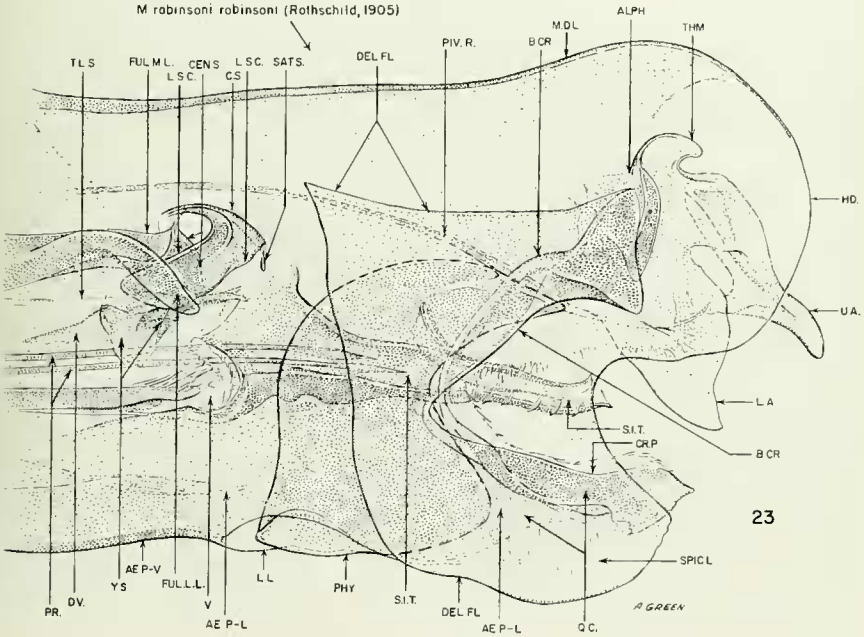


FIGS 18-20
M DRYADOSA N.SP

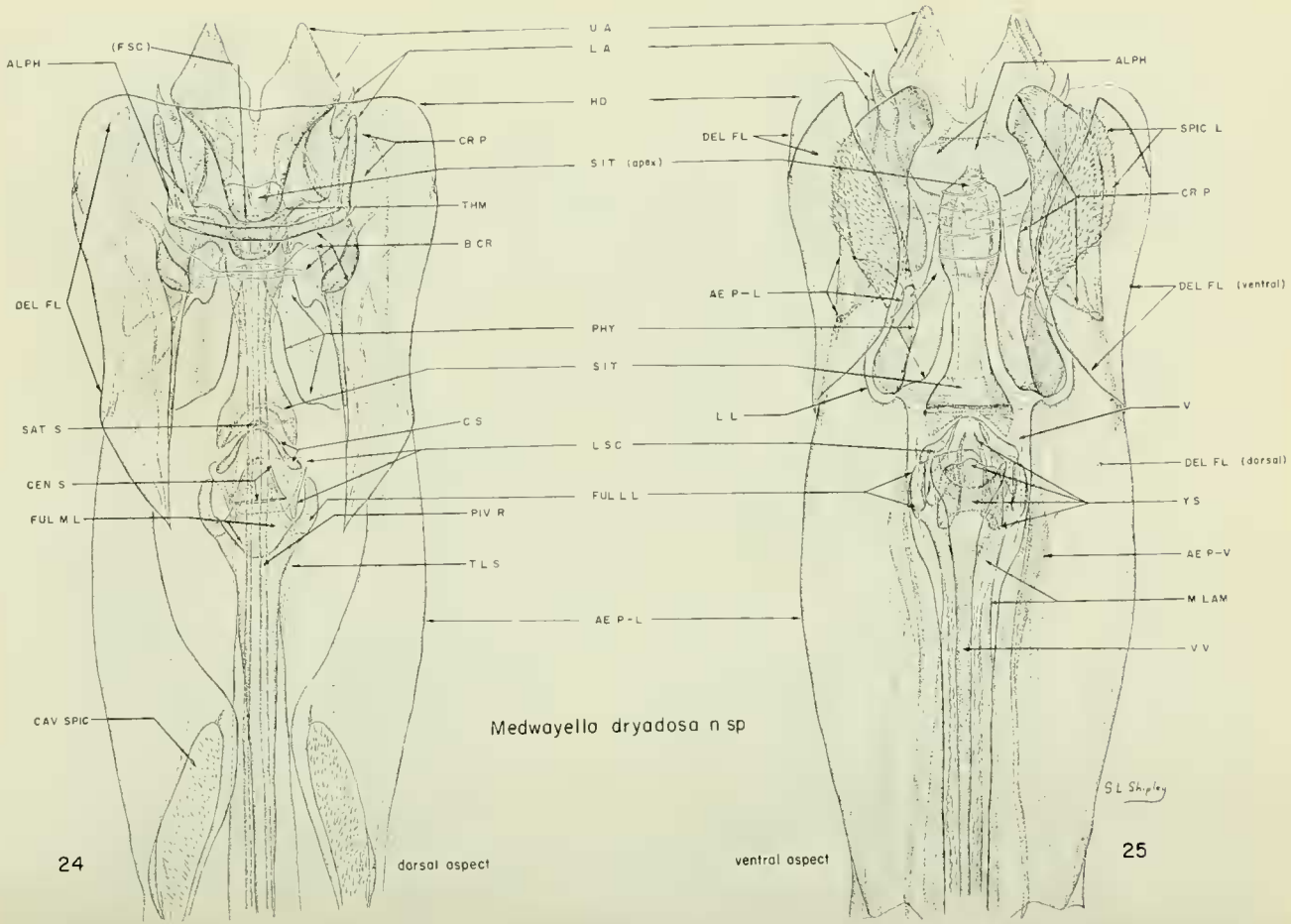
FIG 21
M ROBINSONI ROBINSONI
(ROTHSCHILD, 1905)

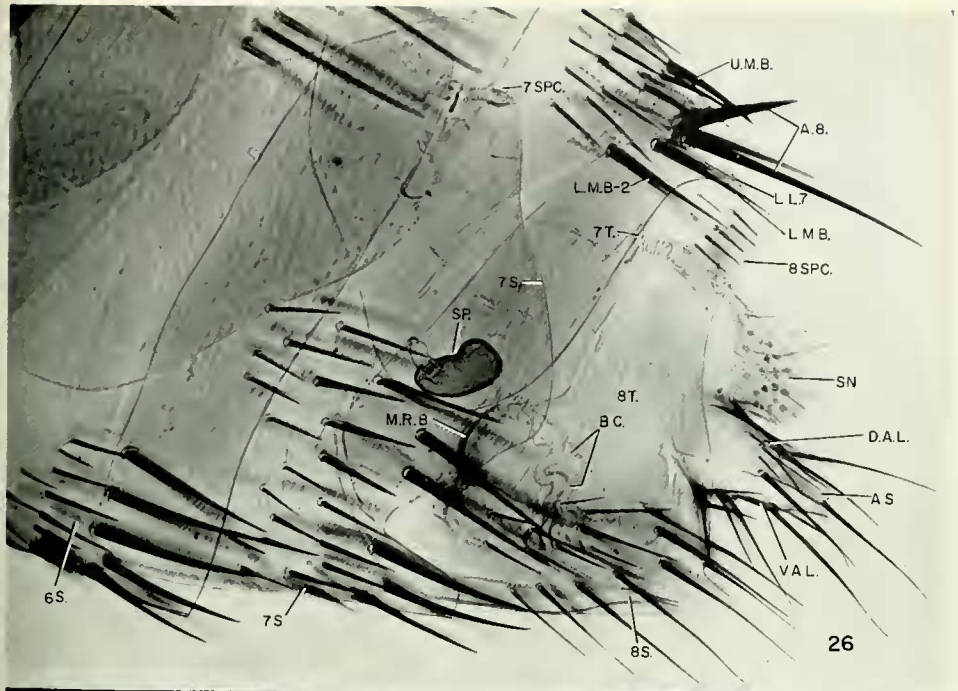

M dryadosa n sp
THM
ALPH
MDL
PIV R
BML
CAV SPIC
CEN S
DEL.FL.
FUL. M.L.
CS.
T.L.S.
PHY
BCR.
BM.L.
SAT S.
HD
SEC
U.A
PIV CD
L A
B CR
CR P
D C.
SPIC L
DEL FL.
S.L. SKIPLEY
D C
PR
M LAM.
L.LAM.
G
APR
PHY.
AE P-L.
S I.T.
LL.
LSC
V
AE P-L.
FUL L L
DV
AE P-V
VV
Y.S.

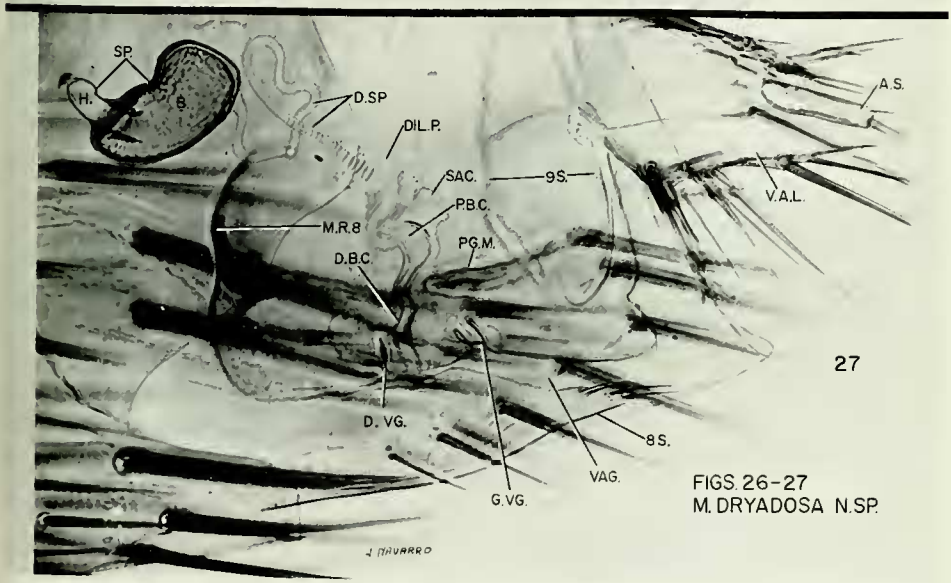
22


M robinsoni robinsoni (Rothschild, 1905)
ALPH
M.DL
THM
PIV. R.
BCR
DEL FL
T.L.S
FUL M.L.
CENS
L.S.C.
LSC.
CS
SATS.
HD.
U.A.
L A
S.I.T.
CR P
B CR
SPIC L
PR.
DV.
AE P-V
YS
FUL L.L.
V
AE P-L
LL
PHY
S.I.T.
DEL FL
AE P-L
Q C.
A GREEN

23


(FSC)
ALPH
DEL FL
SAT S
CEN S
FUL M L
CAV SPIC
CR P
THM
B CR
C S
PIV R
T L S
U A
L A
HD
SIT (apex)
PHY
SIT
L S C
FUL L L
AE P-L
24
dorsal aspect
Medwayella dryadosa n sp
ALPH
DEL FL
AE P-L
L L
SPIC L
CR P
DEL FL (ventral)
V
DEL FL (dorsal)
Y S
AE P-V
M LAM
V V
S L Shipley
ventral aspect
25





FIGS. 26–27
M. DRYADOSA N.SP.

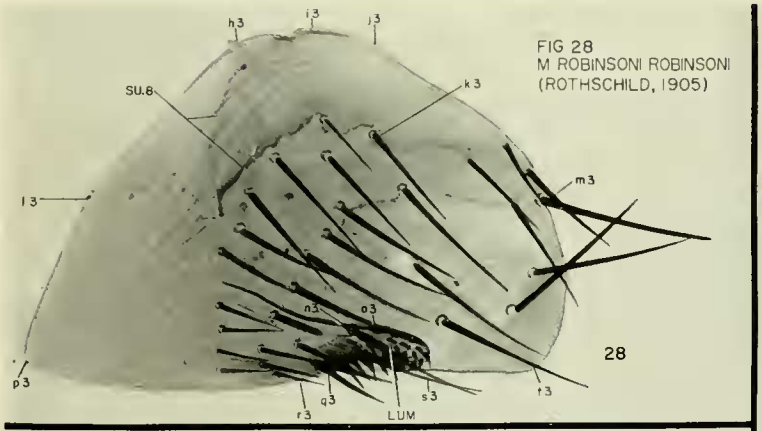
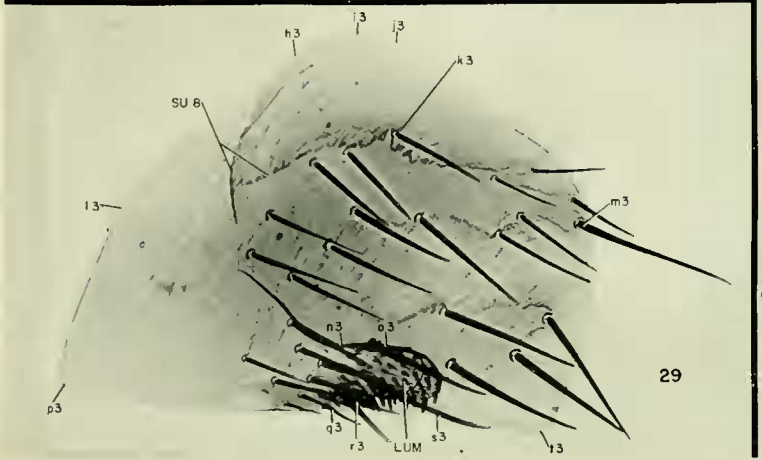
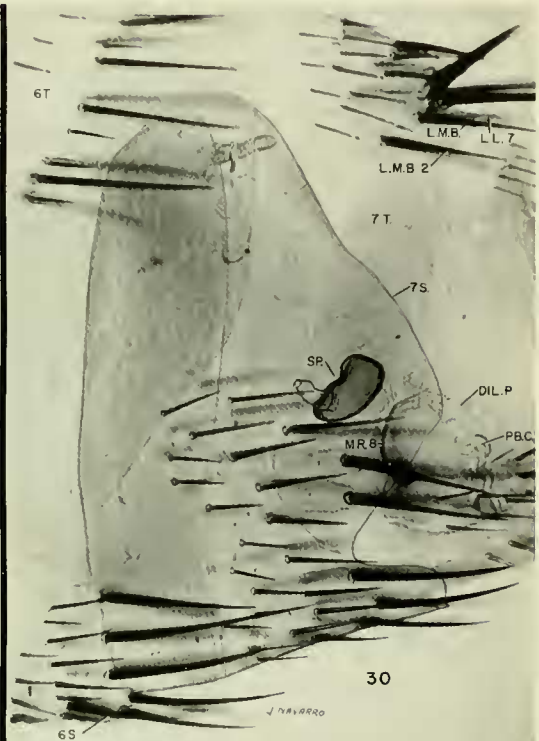
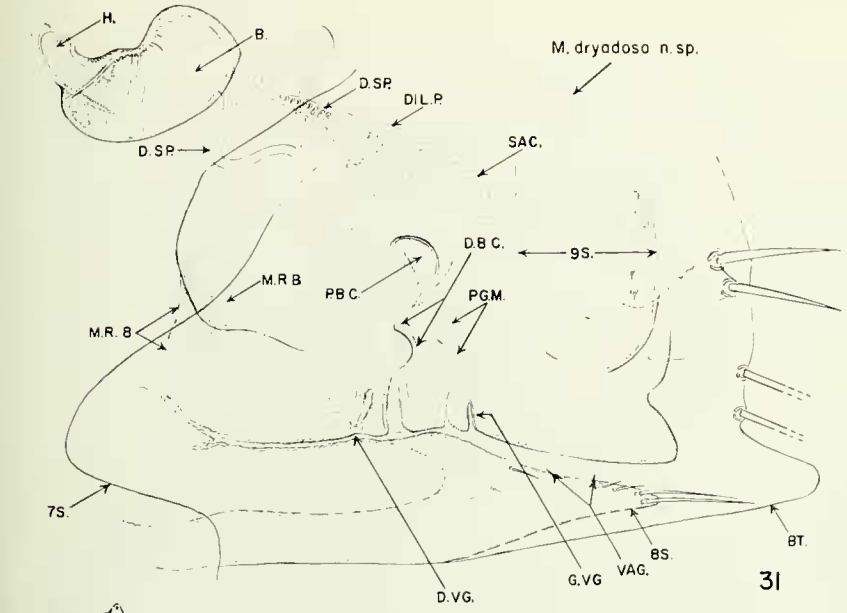


FIG 28
M ROBINSONI ROBINSONI
(ROTHSCHILD, 1905)

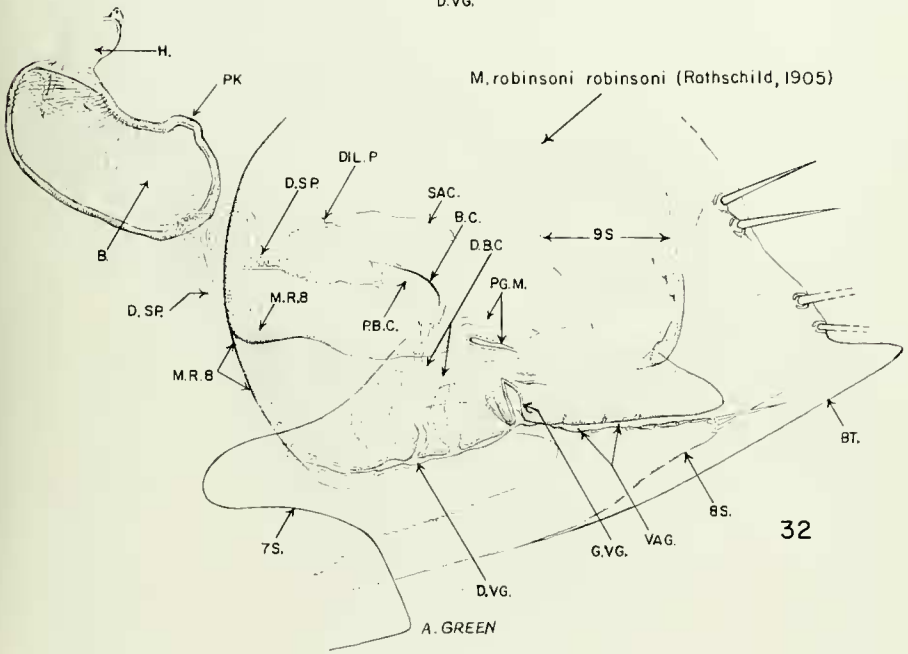




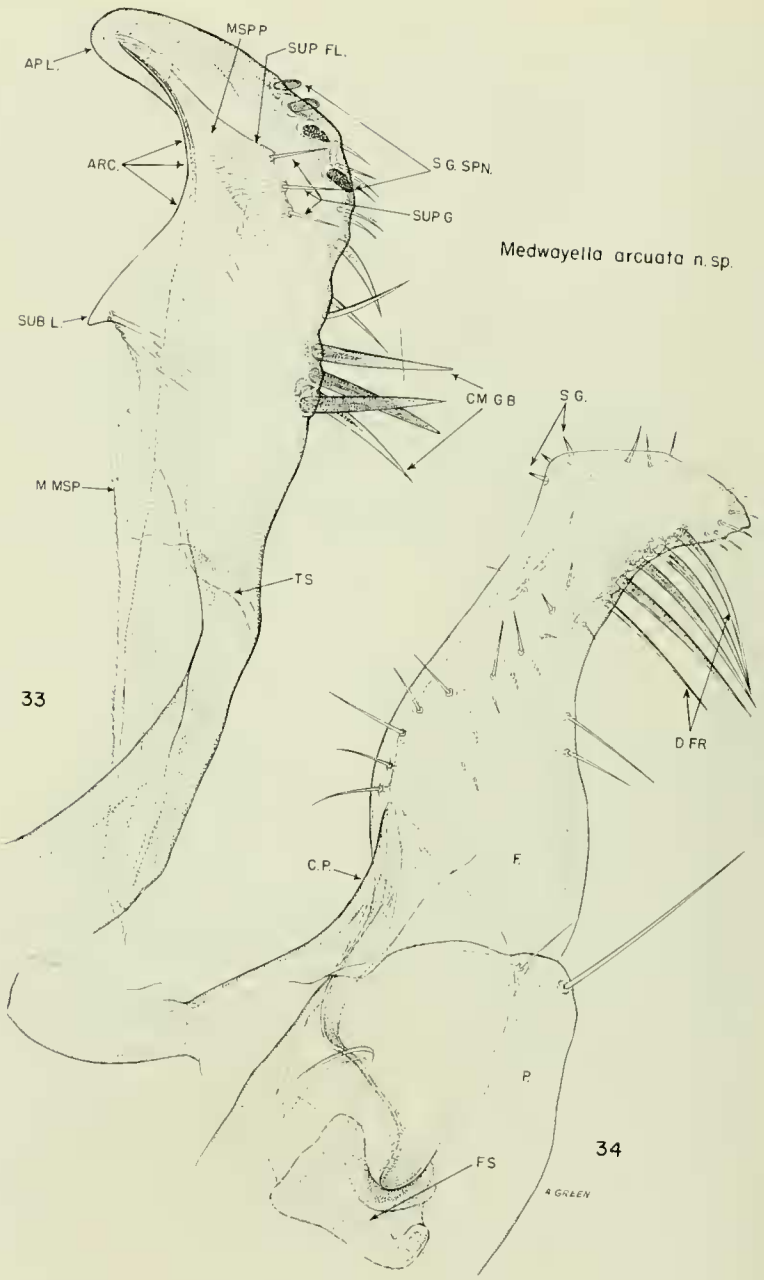
FIGS 29-30
M. DRYADOSA N SP

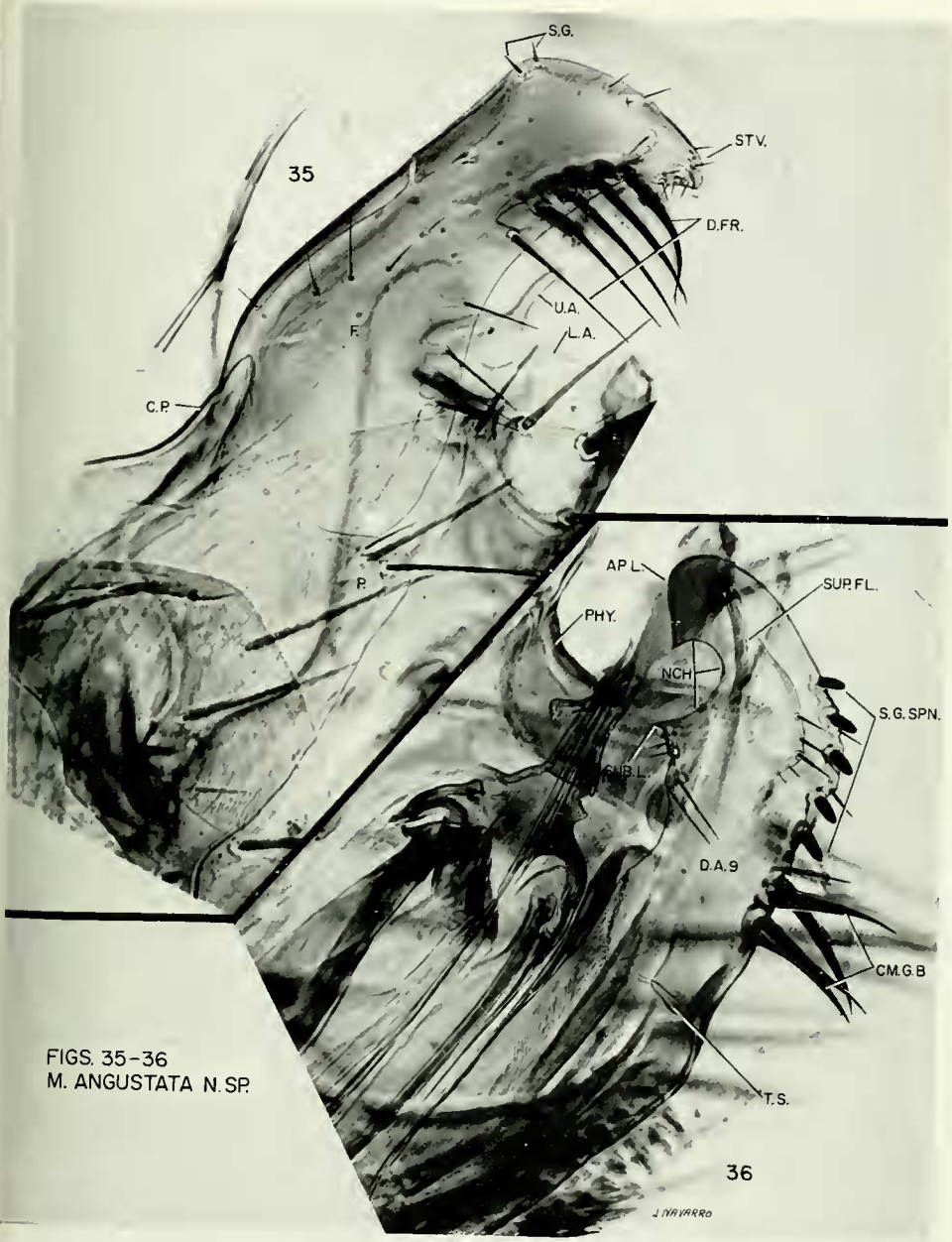

H.
B.
D.SP.
DIL.P.
D.SP.
M. dryadoso n. sp.
SAC.
D.B.C.
9S.
M.R.B.
P.B.C.
PG.M.
M.R. 8
7S.
8S.
8T.
D.VG.
G.VG
VAG.

31


H.
PK
M. robinsoni robinsoni (Rothschild, 1905)
DIL. P
D.S.P.
SAC.
B.C.
B.
9S
D.B.C
PG.M.
D. SP.
M.R.B
P.B.C.
M.R. 8
8T.
8S.
7S.
G.VG.
VAG.
D.VG.
A. GREEN

32


MSP P
SUP FL.
AP L.
ARC.
S G. SPN.
SUP G
Medwayella arcuata n. sp.
SUB L.
CM G B
S G.
M MSP
TS
33
D FR
C.P.
F.
P.
34
FS
A GREEN



FIGS. 35–36
M. ANGUSTATA N. SP.

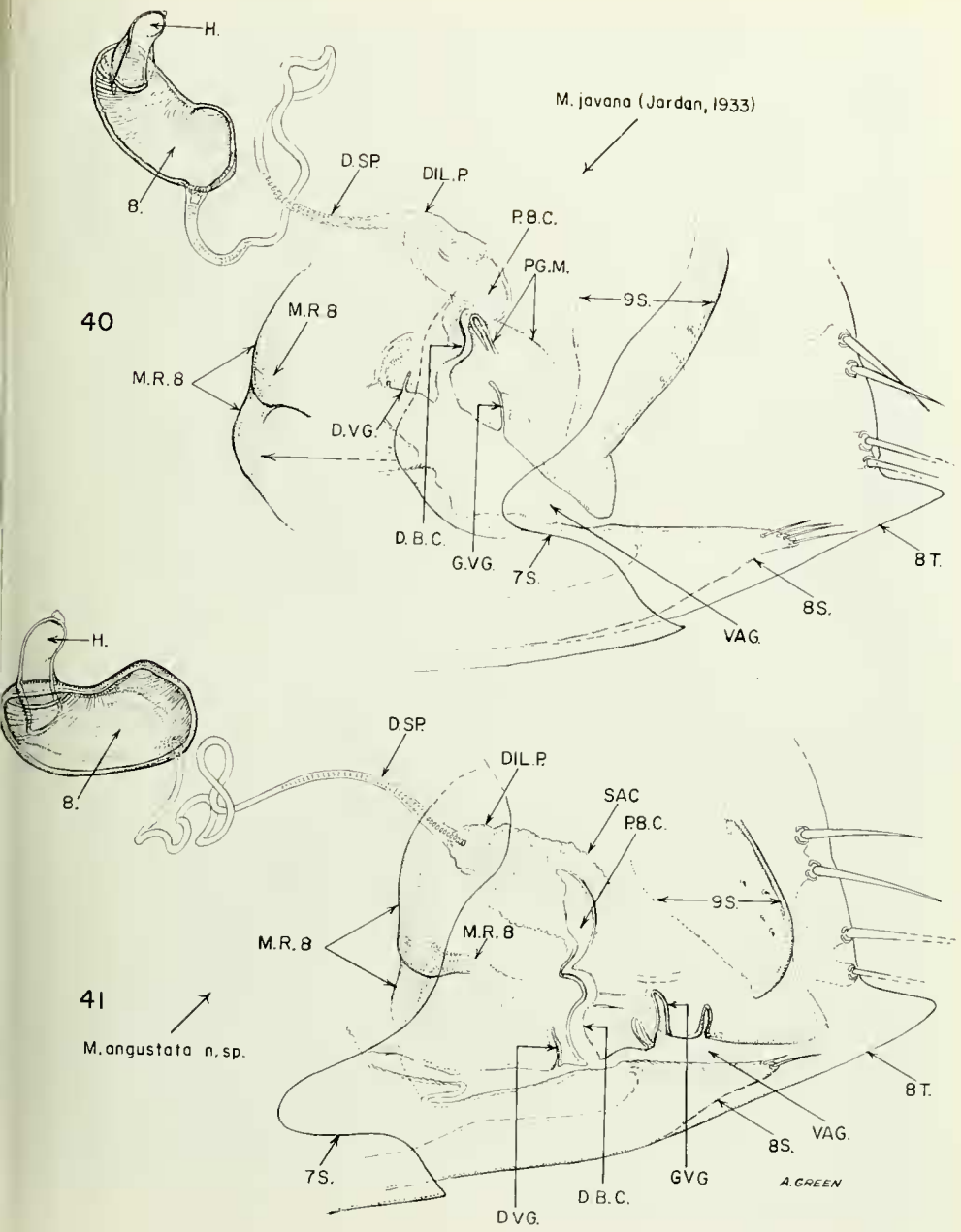
37

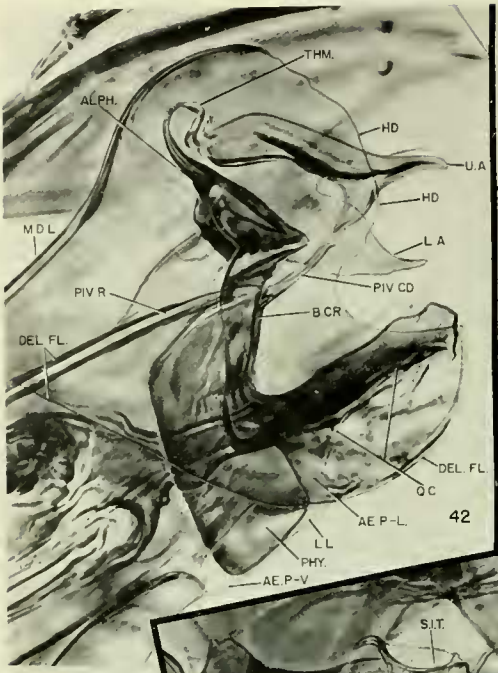
38

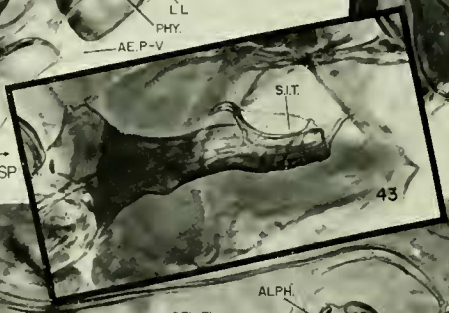
39

FIGS. 37–39
M. ANGUSTATA N SP

J. NAVARRO


H.
8.
M. javana (Jordan, 1933)
D.SP.
DIL.P.
P.B.C.
PG.M.
9S.
40
M.R.8
M.R.8
D.VG.
D.B.C.
G.VG.
7S.
8T.
8S.
VAG.
H.
8.
D.SP.
DIL.P.
SAC
P.B.C.
9S.
M.R.8
M.R.8
41
M. angustata n. sp.
8T.
VAG.
8S.
7S.
GVG
D.B.C.
DVG.
A.GREEN





FIGS 42-43
M DRYADOSA N SP

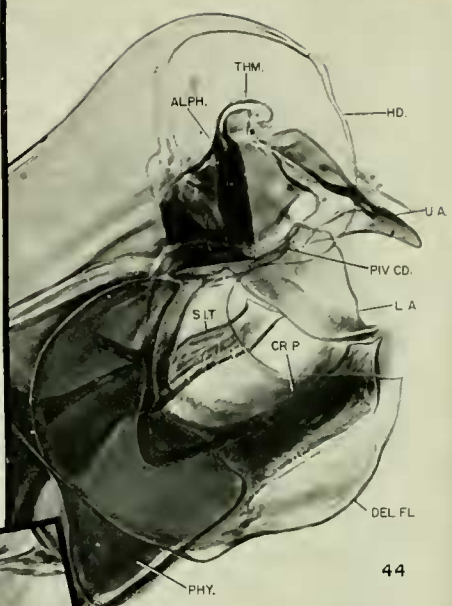


FIG 44
M ROBINSONI ROBINSONI
(ROTHSCHILD, 1905)

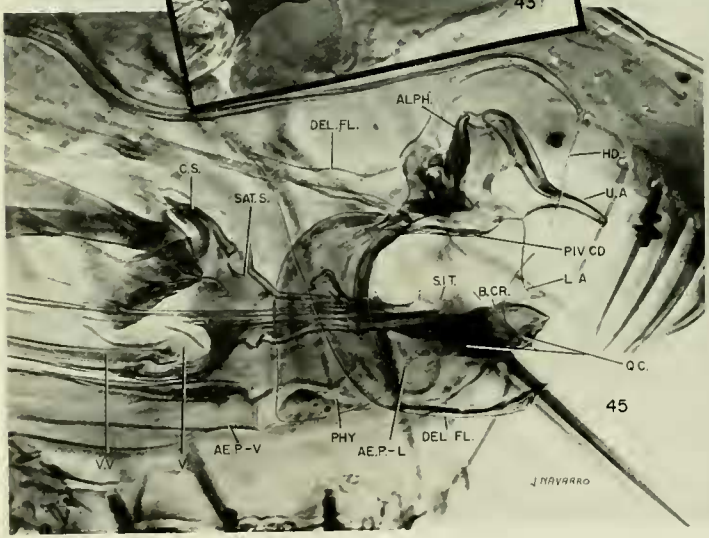
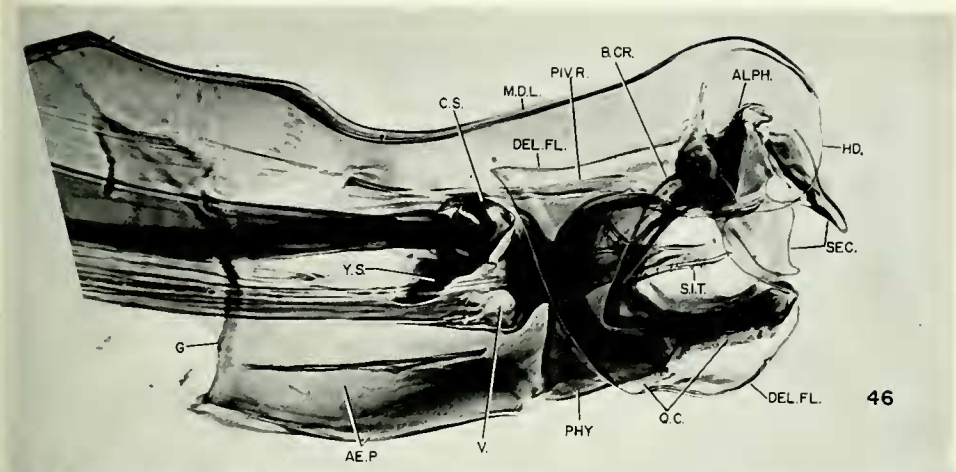
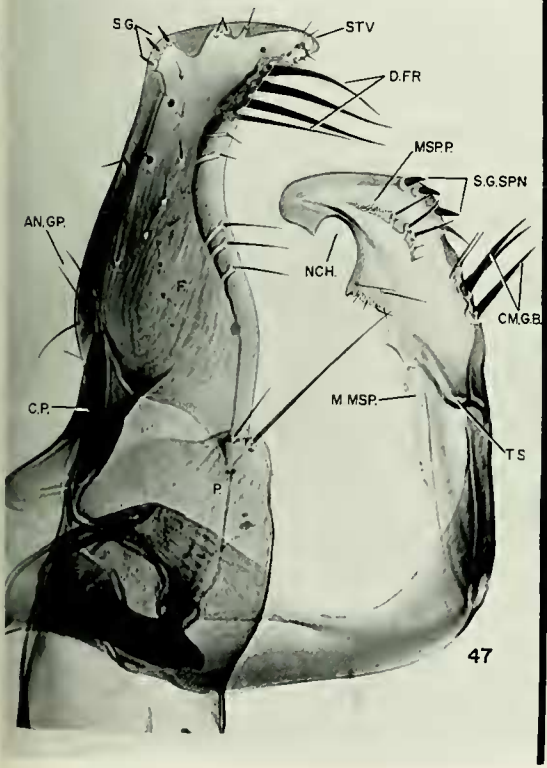
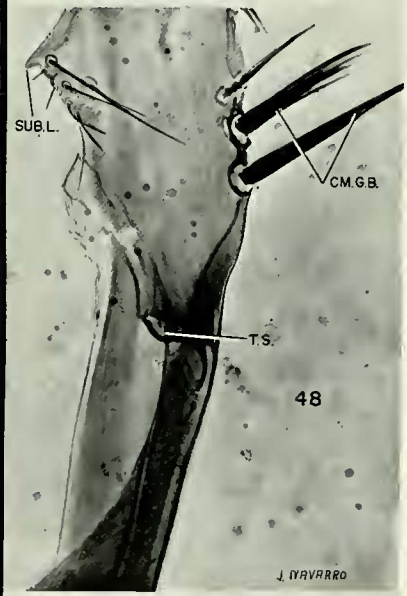


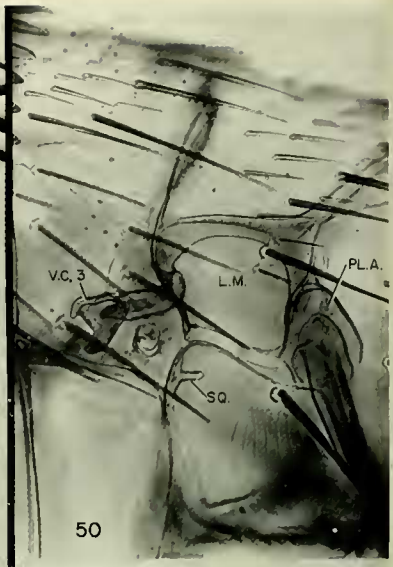
FIG 45
M ANGUSTATA N SP



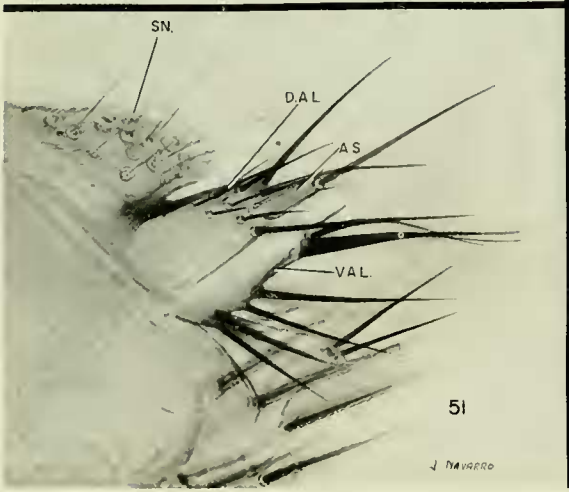


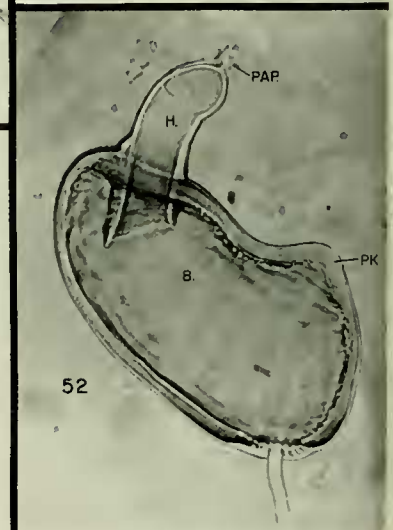


FIGS. 46-48
M. ROBINSONI ROBINSONI
(ROTHSCHILD, 1905)



FIGS. 49–52
M. ROBINSONI ROBINSONI
(ROTHSCHILD, 1905)





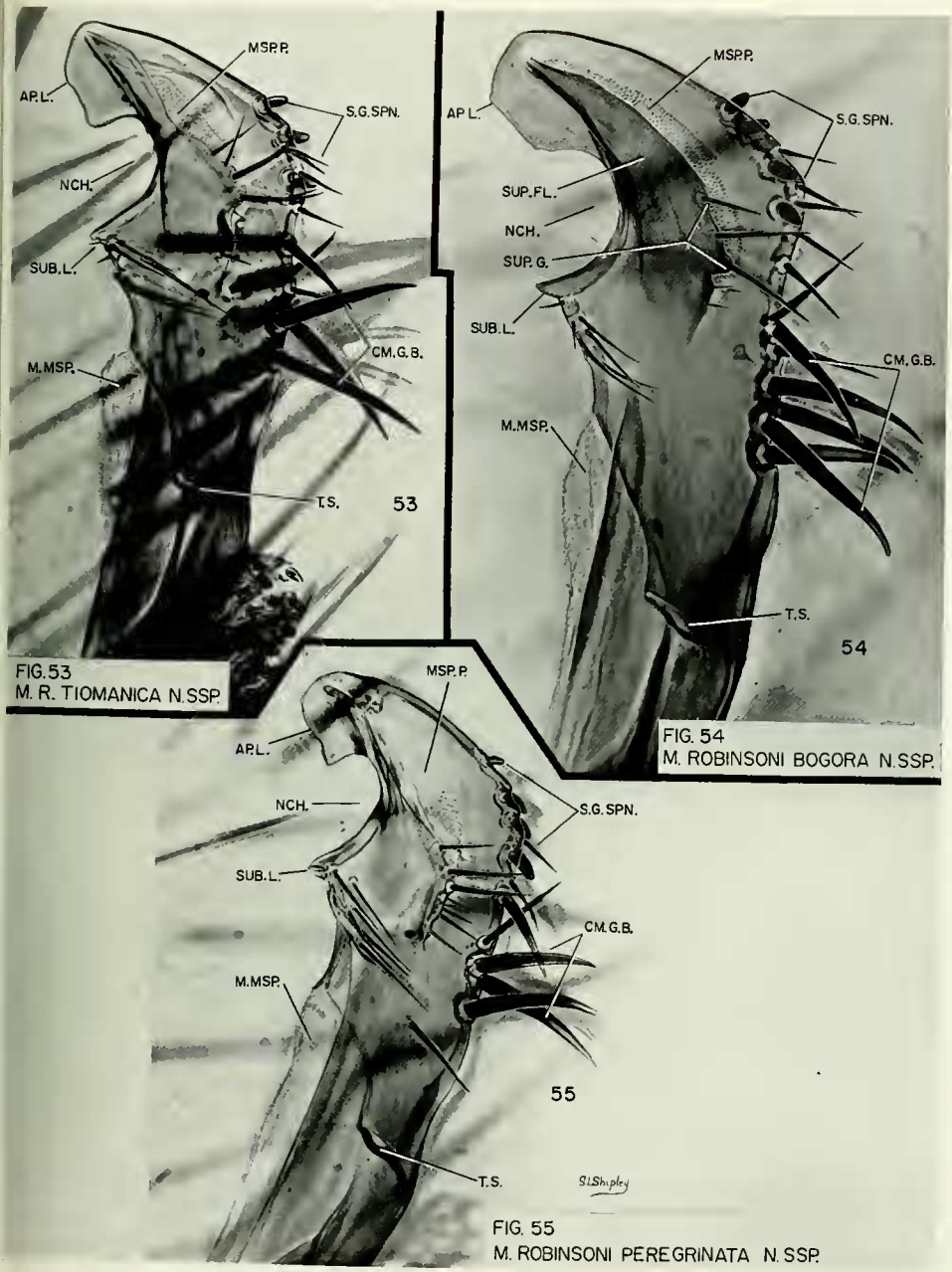
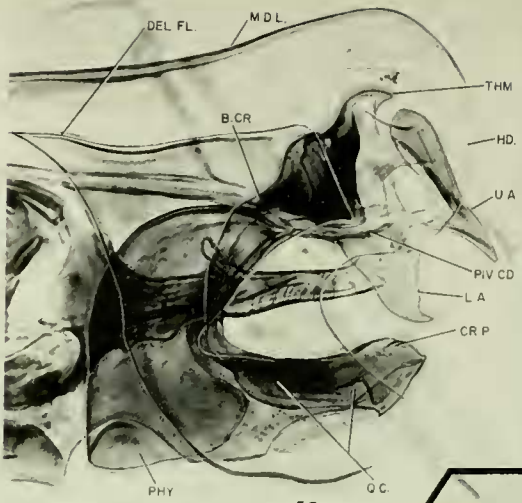


FIG. 53
M. R. TIOMANICA N.SSP.

FIG. 54
M. ROBINSONI BOGORA N.SSP.

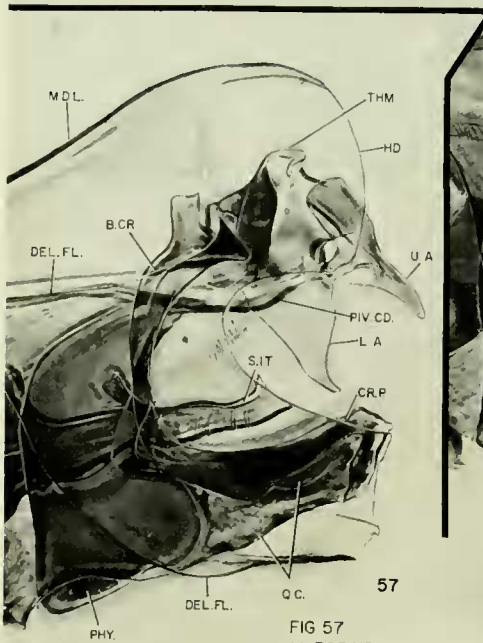
FIG. 55
M. ROBINSONI PEREGRINATA N. SSP.



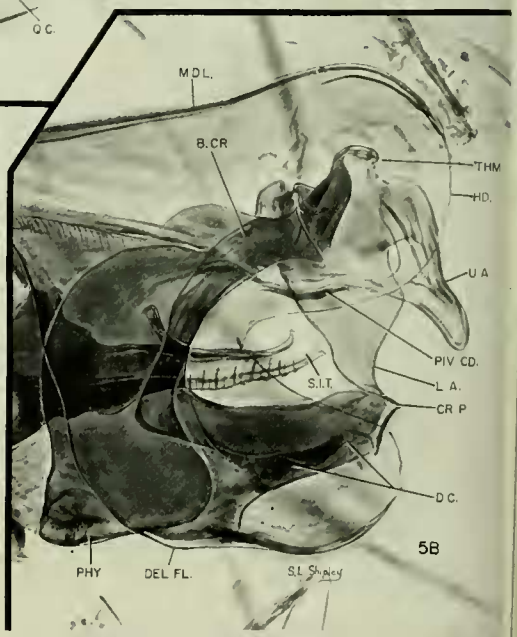
56

← FIG 56
M. ROBINSONI TIOMANICA N SSP

FIG 58
M ROBINSONI BOGORA N SSP
↓



57



58

FIG 57
M ROBINSONI PEREGRINATA N SSP

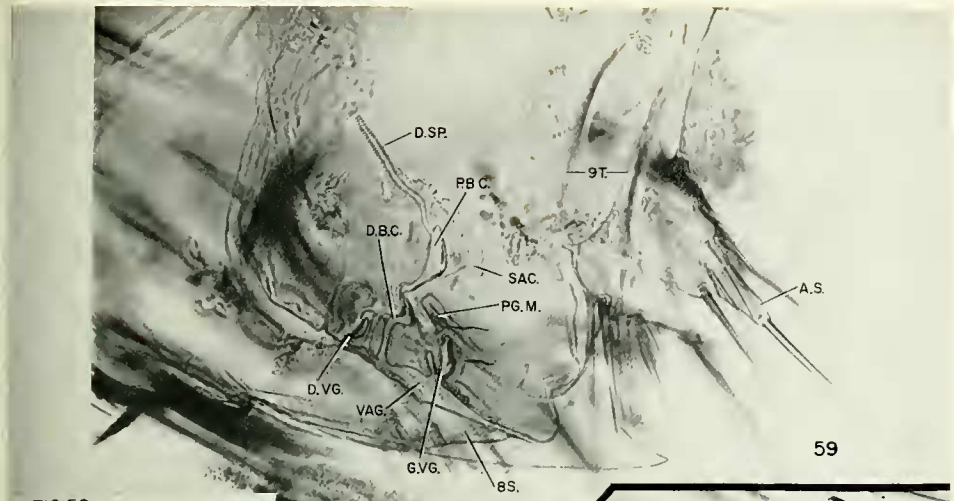
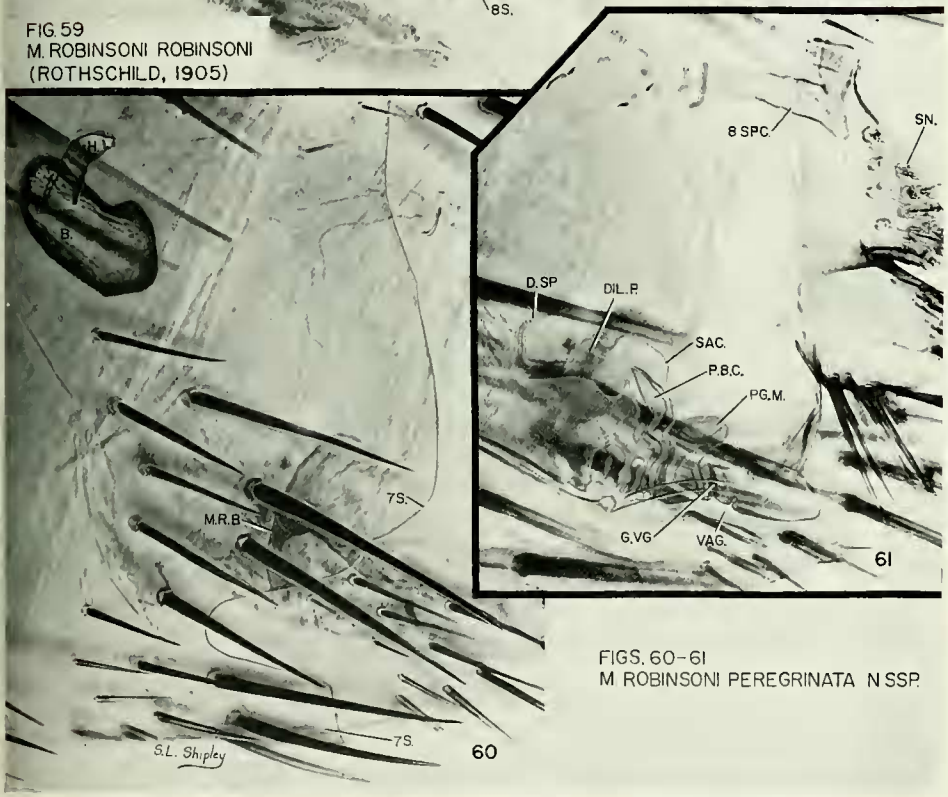
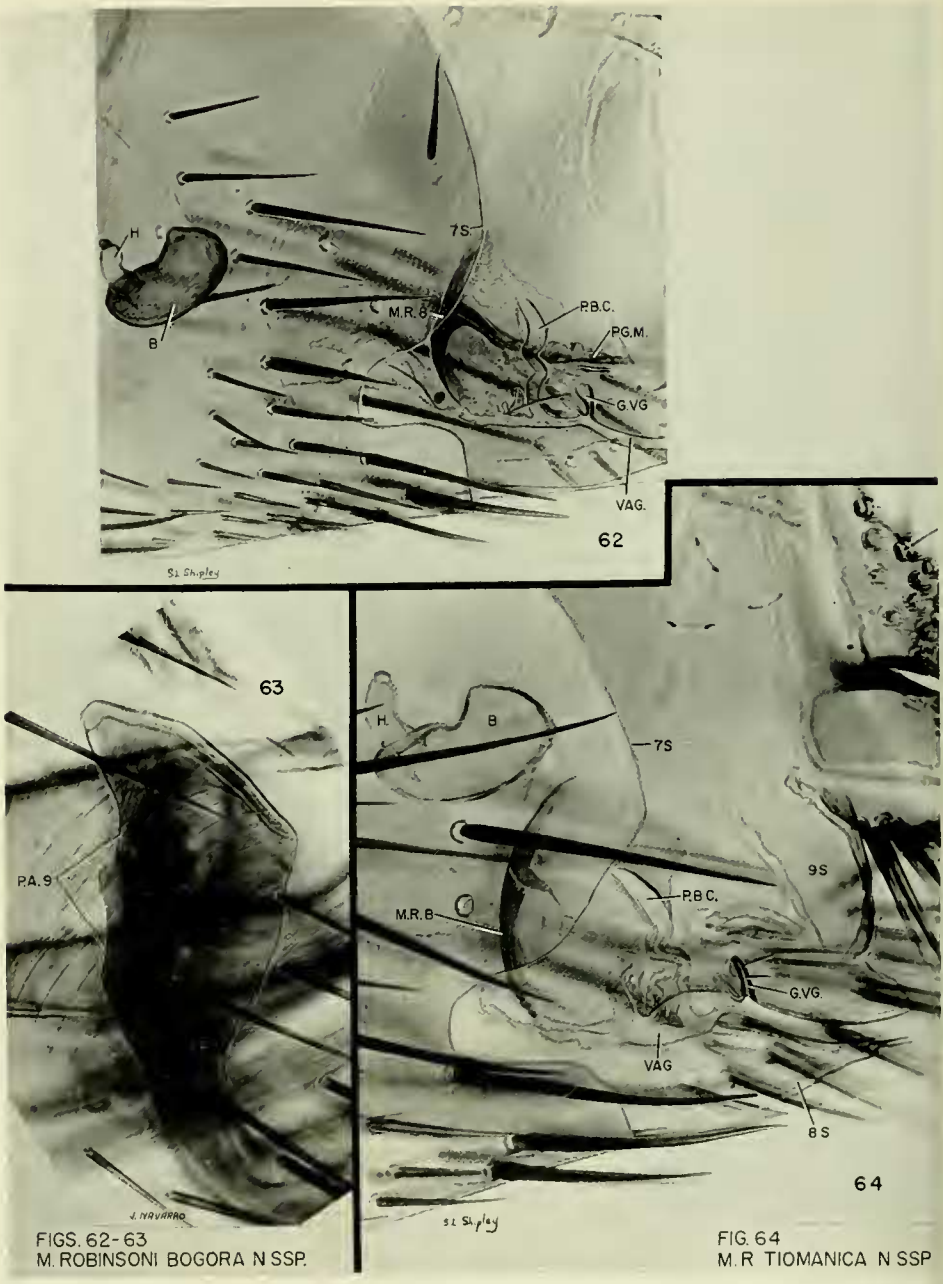


FIG. 59
M. ROBINSONI ROBINSONI
(ROTHSCHILD, 1905)

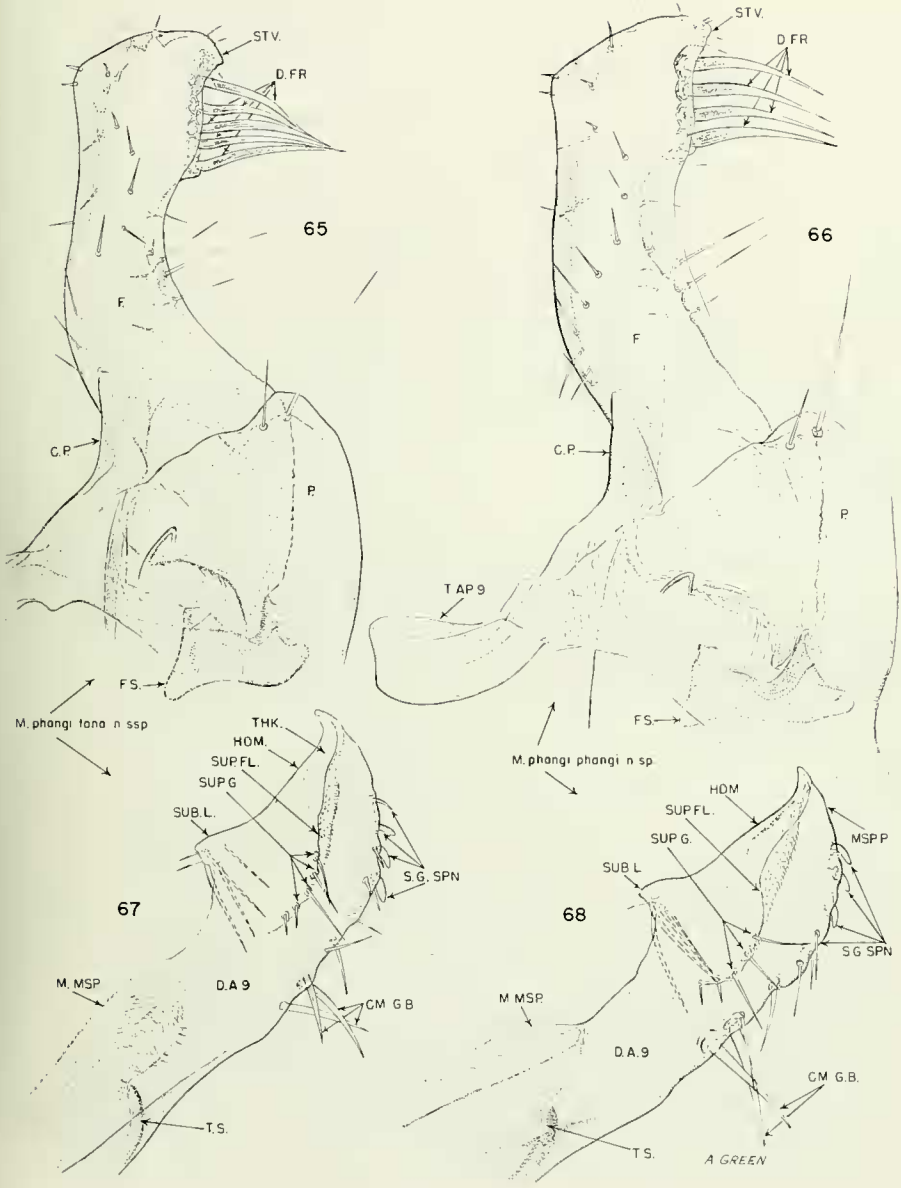


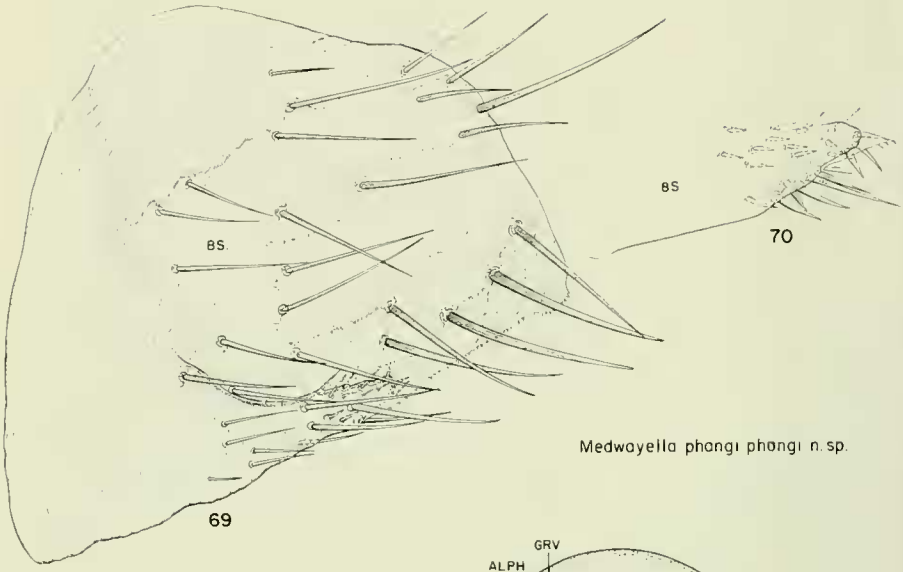
FIGS. 60–61
M. ROBINSONI PEREGRINATA N SSP.



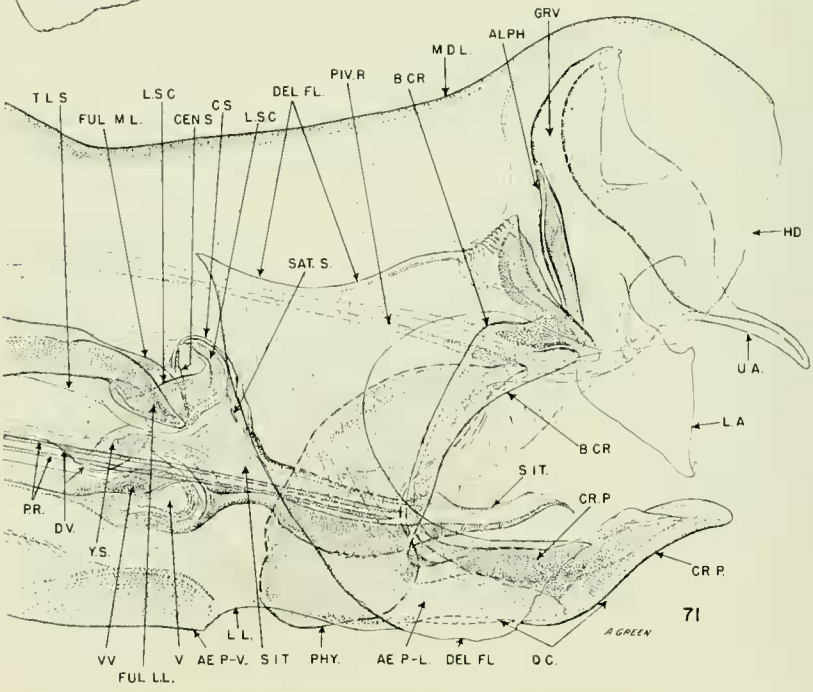
FIGS. 62-63
M. ROBINSONI BOGORA N SSP.

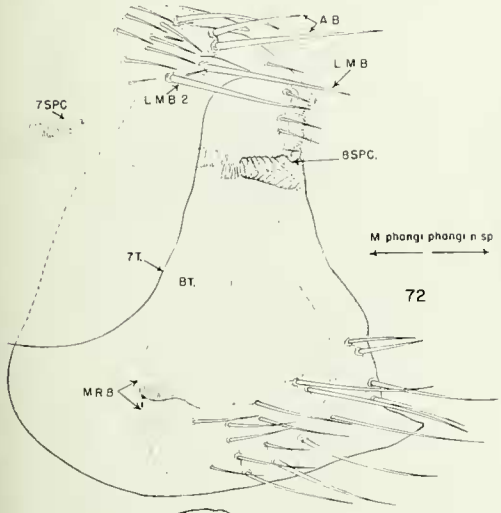
FIG. 64
M. R TIOMANICA N SSP

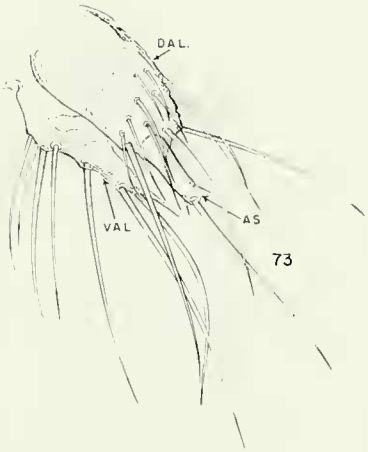

STV.
D.FR
65
F.
C.P.
P.
F.S.
M. phangi fana n ssp
THK.
HOM.
SUP.FL.
SUP.G.
SUB.L.
S.G. SPN
67
M. MSP.
D.A.9
CM G.B.
T.S.
STV.
D.FR
66
F.
C.P.
P.
T.AP.9
F.S.
M. phangi phangi n sp.
HOM.
SUP.FL.
SUP.G.
MSP.P.
SUB.L.
S.G. SPN
68
M. MSP.
D.A.9
CM G.B.
T.S.
A. GREEN

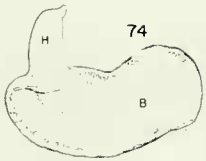


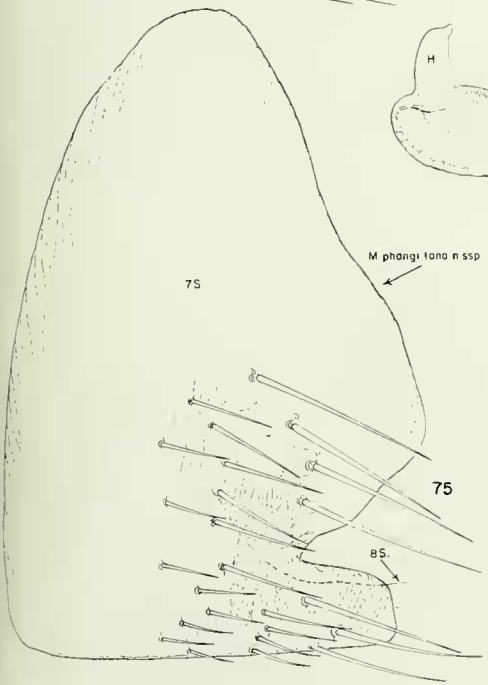
Medwayella phongi phongi n. sp.

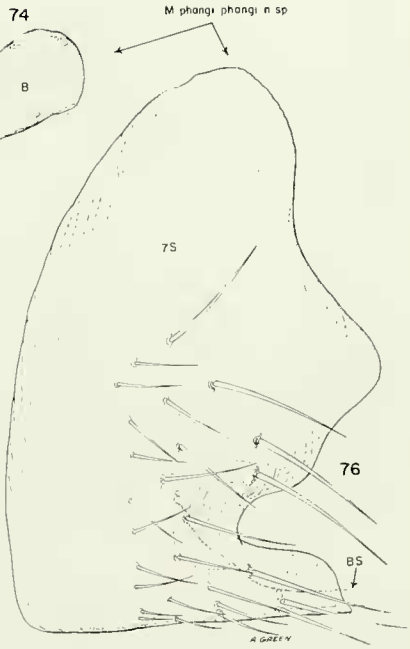


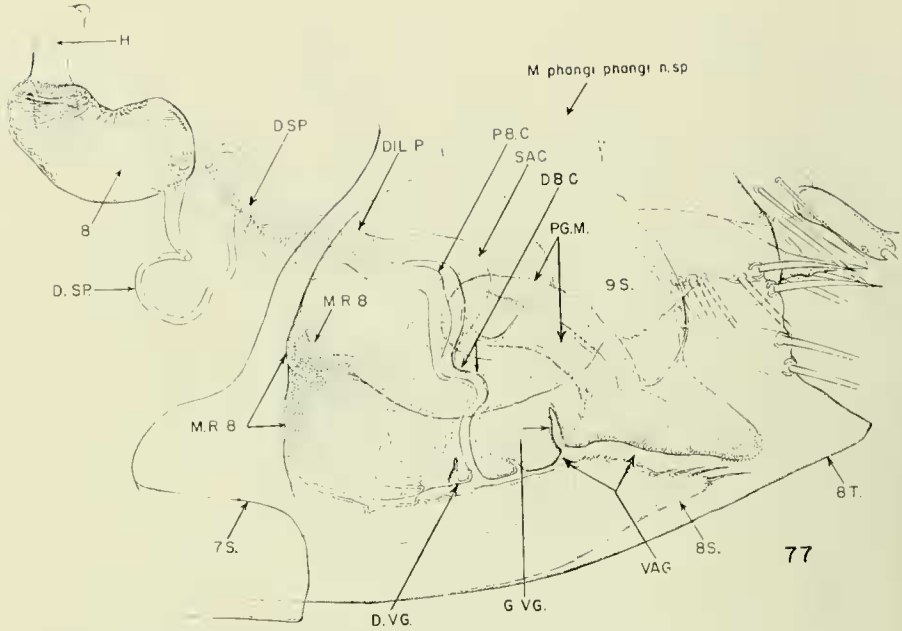

AB
LMB
LMB 2
7SPC
8SPC.
M phangi phangi n sp
7T.
BT.
72
MRB

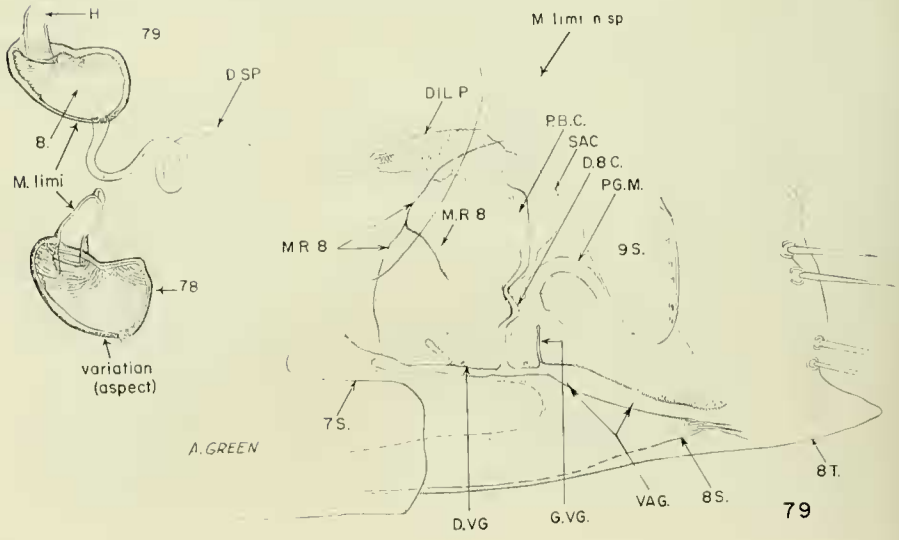

DAL.
VAL
AS
73

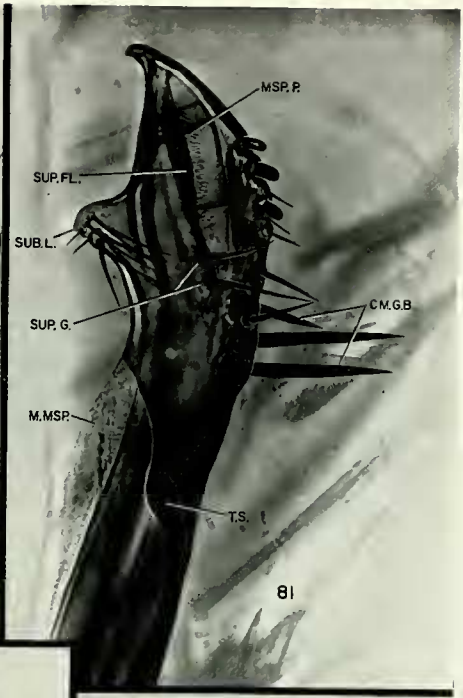

H
74
B

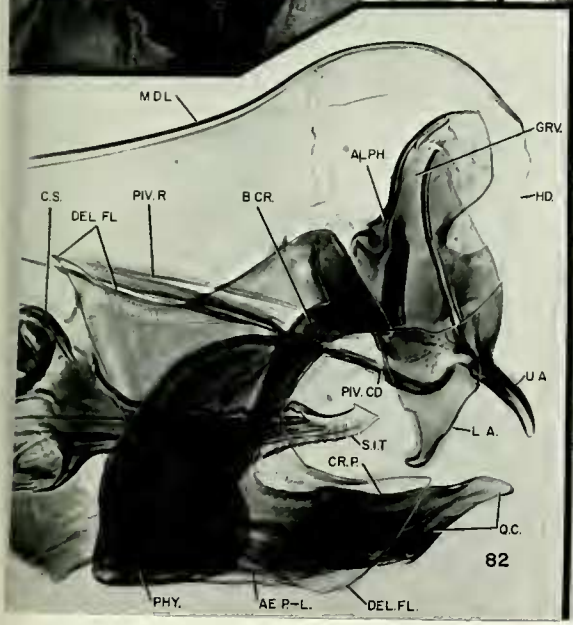

M phangi tana n ssp
7S
75
BS.

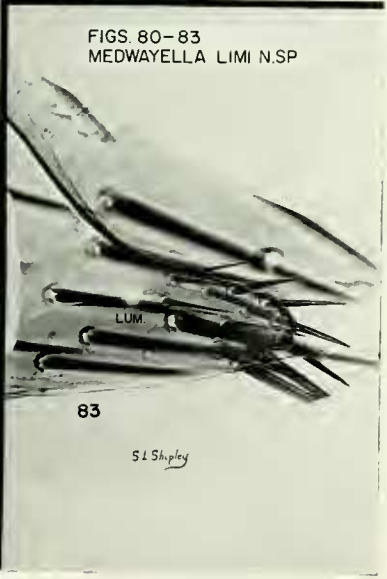

M phangi phangi n sp
7S
76
BS
A GREEN


H
8
D. SP.
DSP
DIL P
P.B.C
SAC
D.8.C
PG.M.
9S.
M phongi phongi n.sp
M.R 8
M.R 8
7S.
D.VG.
G VG.
VAG
8S.
8T.
77

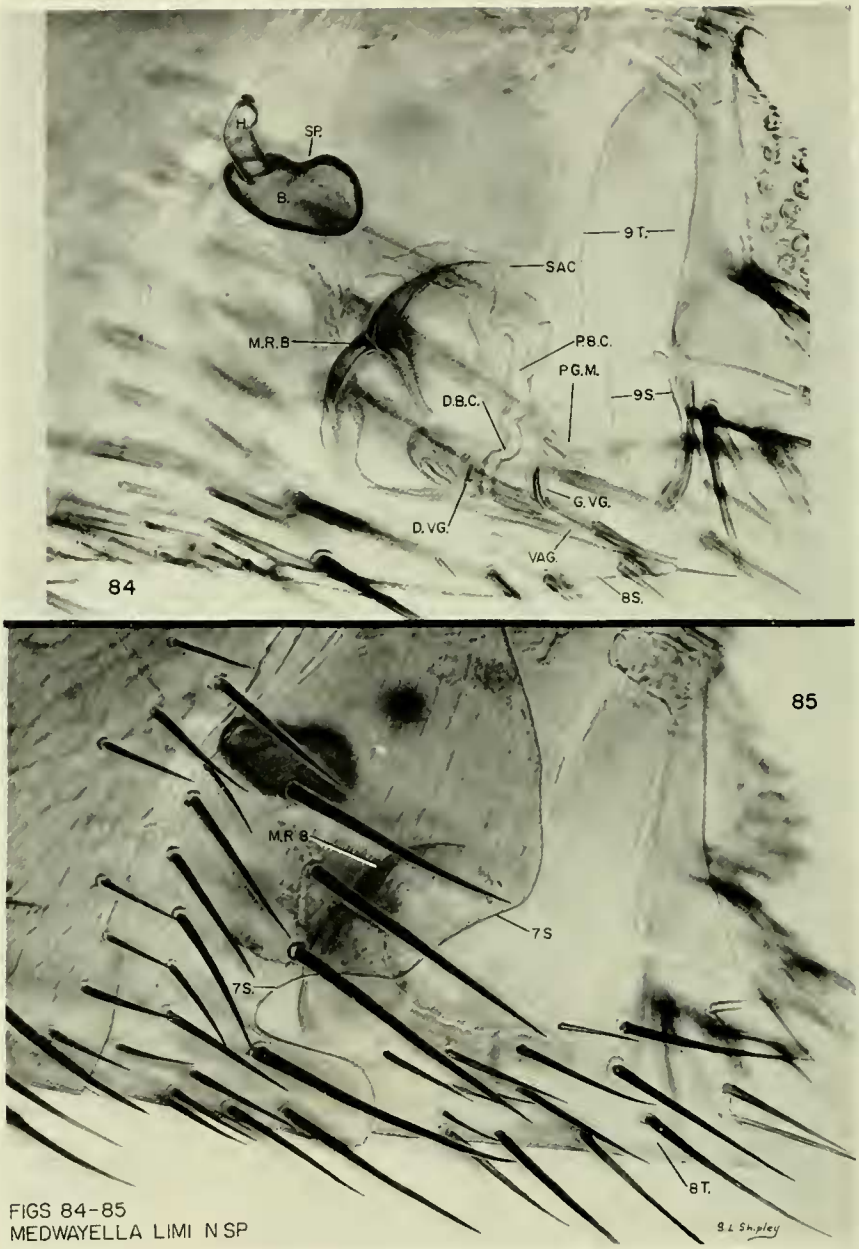

H
79
8.
M. limi
78
variation
(aspect)
DSP
M limi n sp
DIL P
P.B.C.
SAC
D.8.C.
PG.M.
M.R 8
M.R 8
9S.
7S.
D.VG
G.VG.
VAG.
8S.
8T.
79
A. GREEN



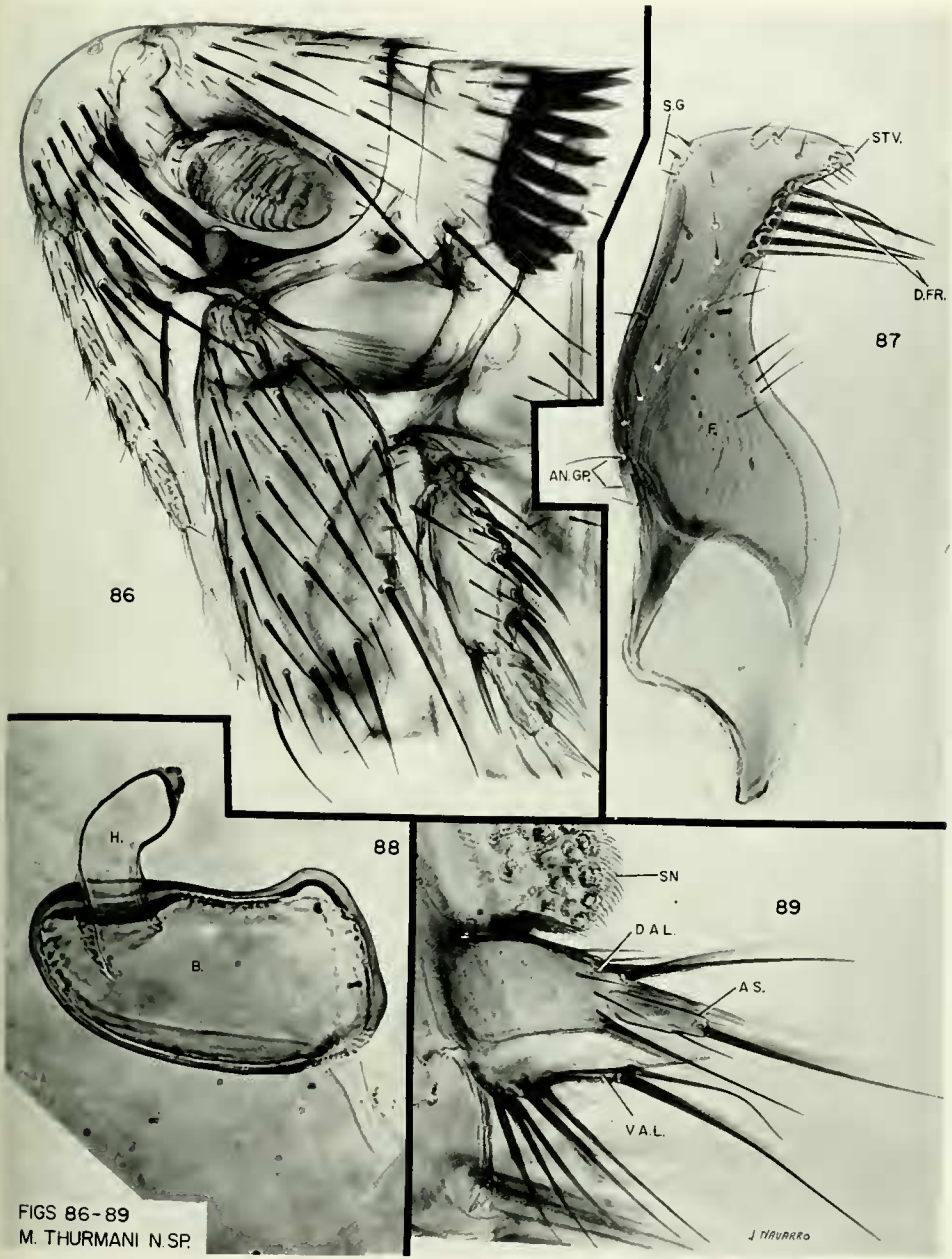




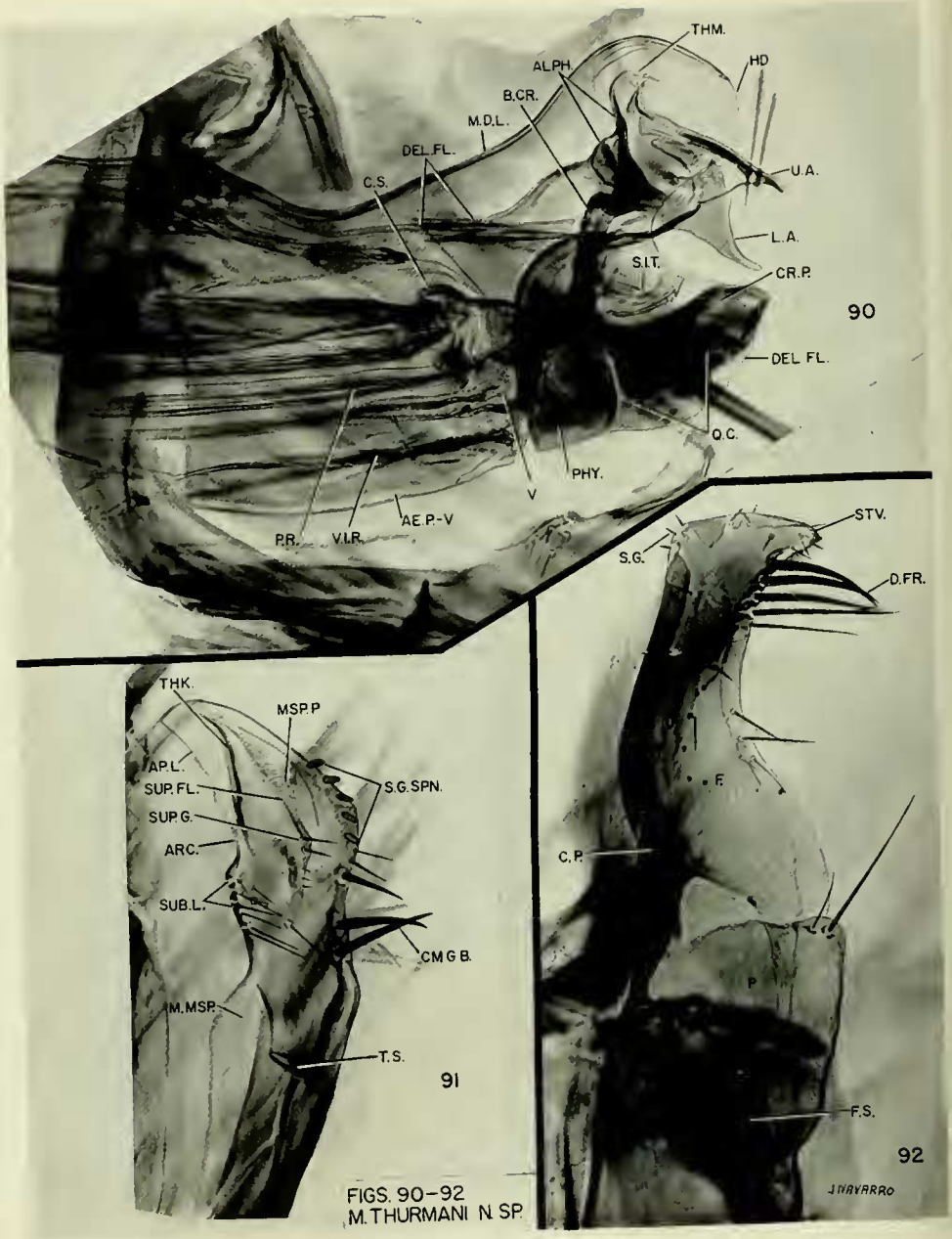
FIGS. 80–83
MEDWAYELLA LIMI N.SP



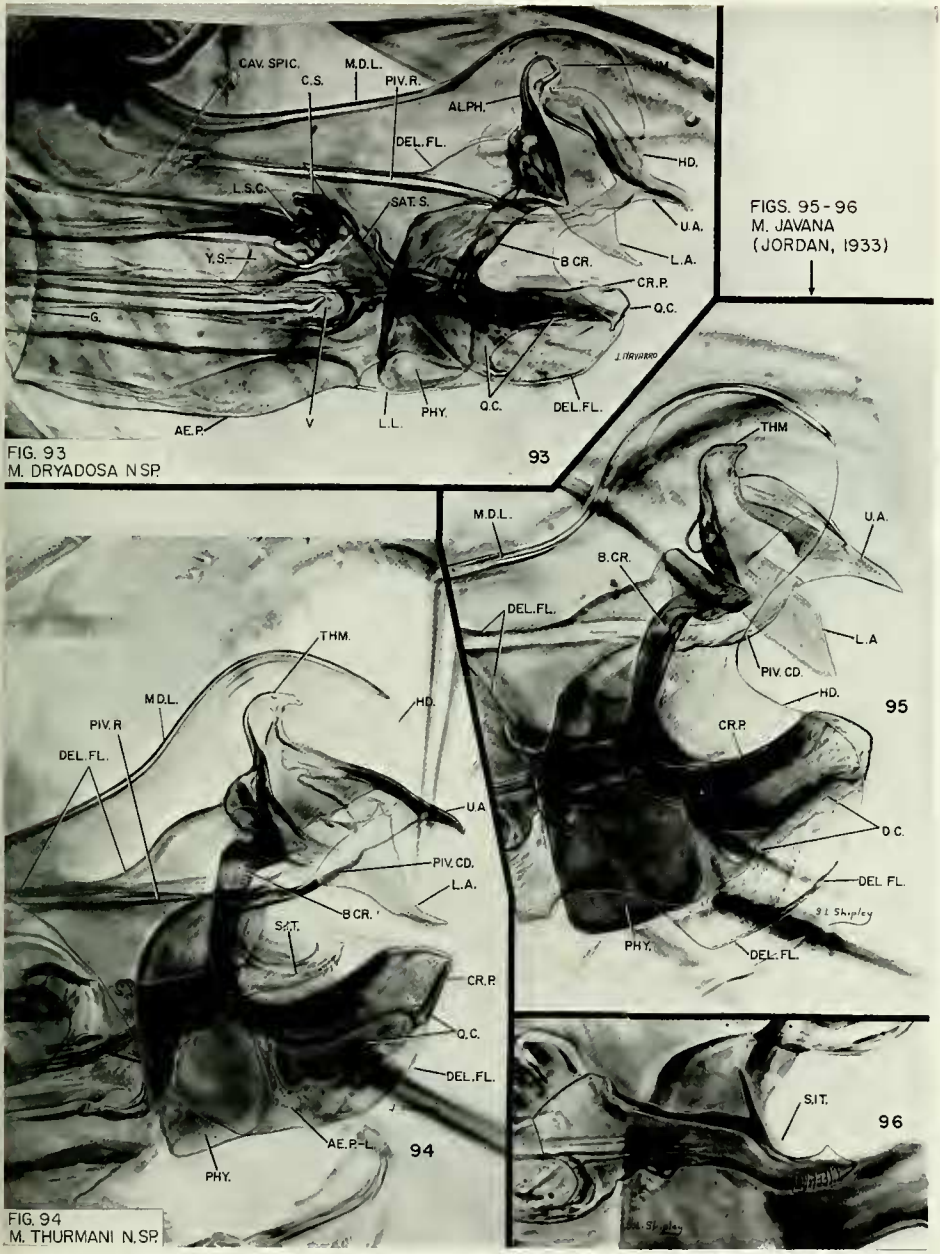
FIGS 84-85
MEDWAYELLA LIMI N SP



FIGS 86-89
M. THURMANI N.SP.



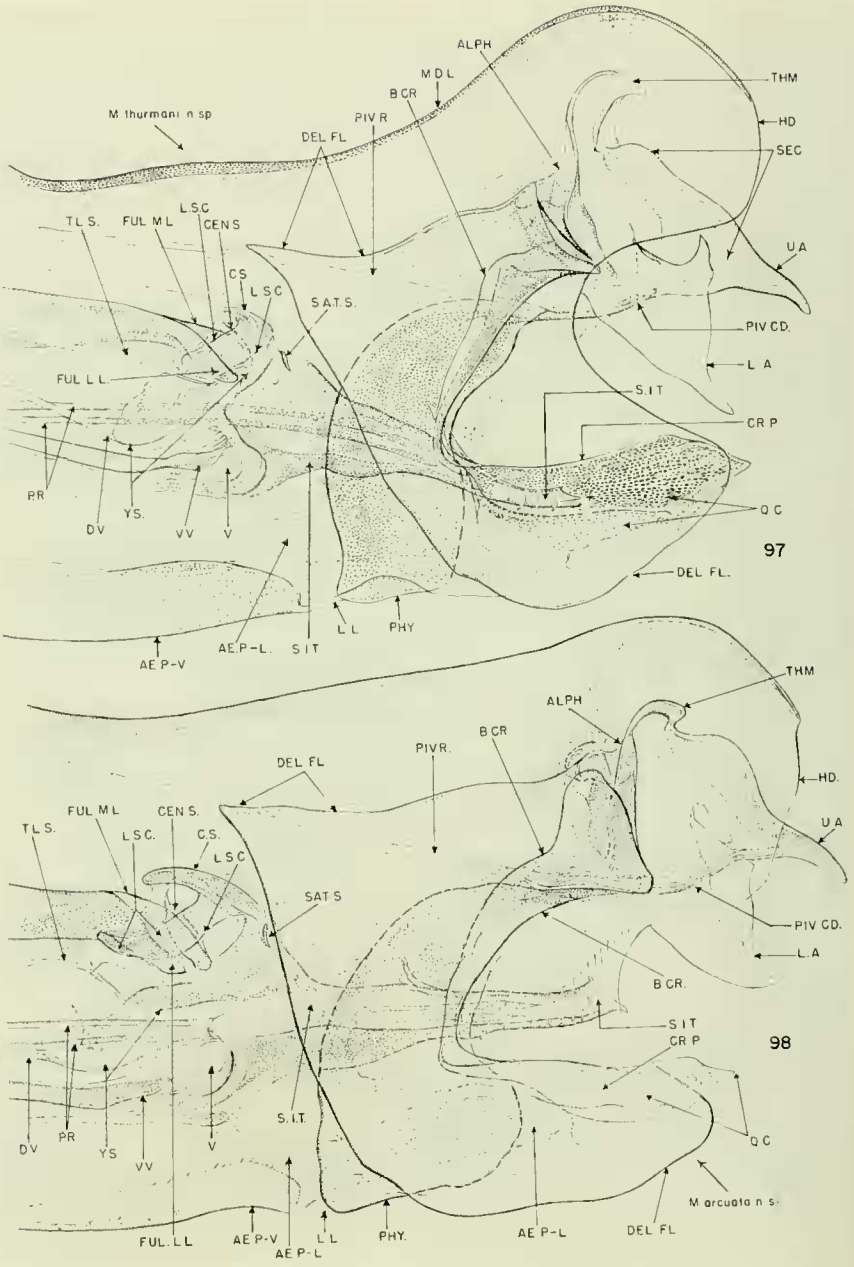
FIGS. 90–92
M. THURMANI N. SP.

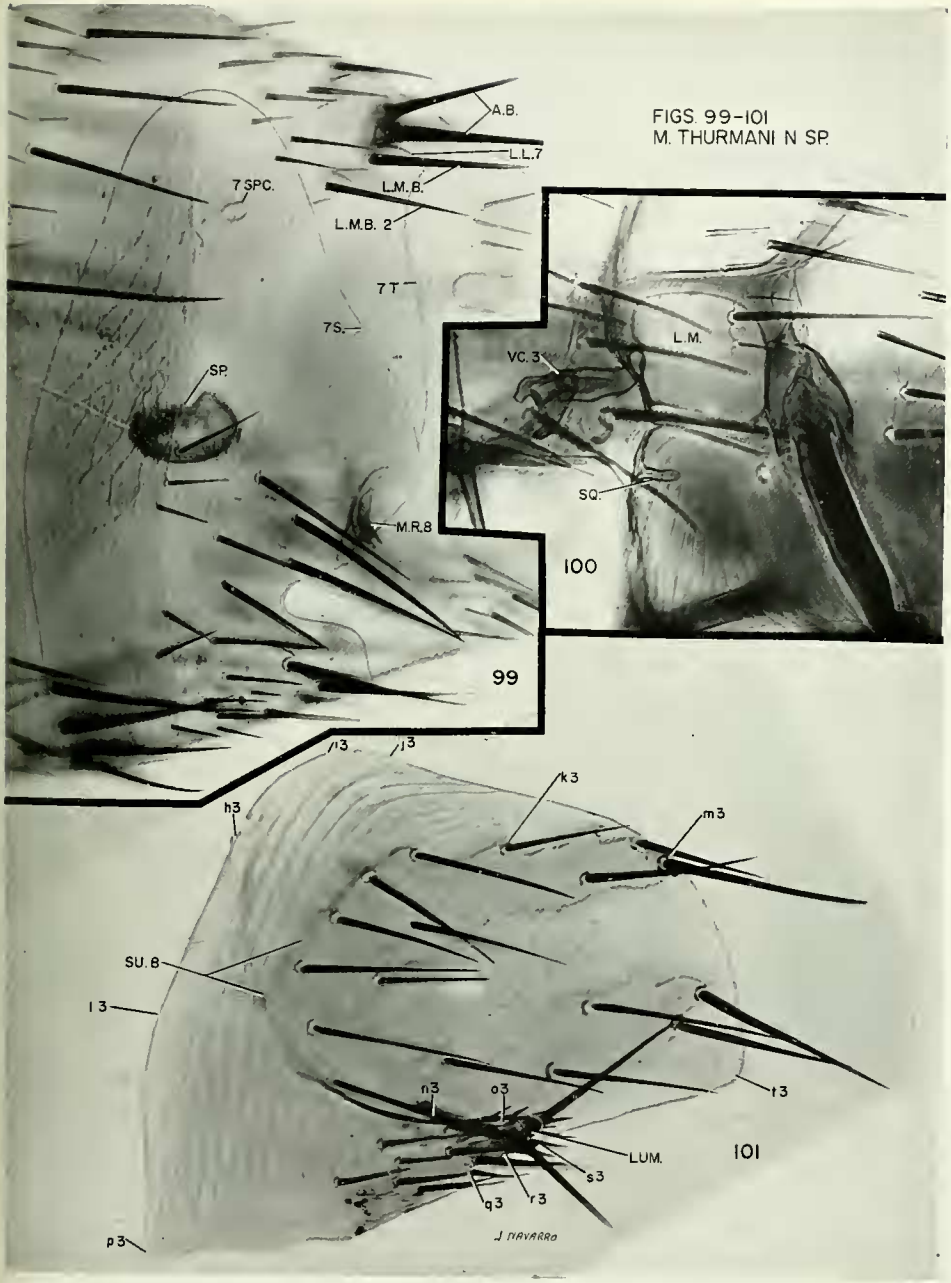


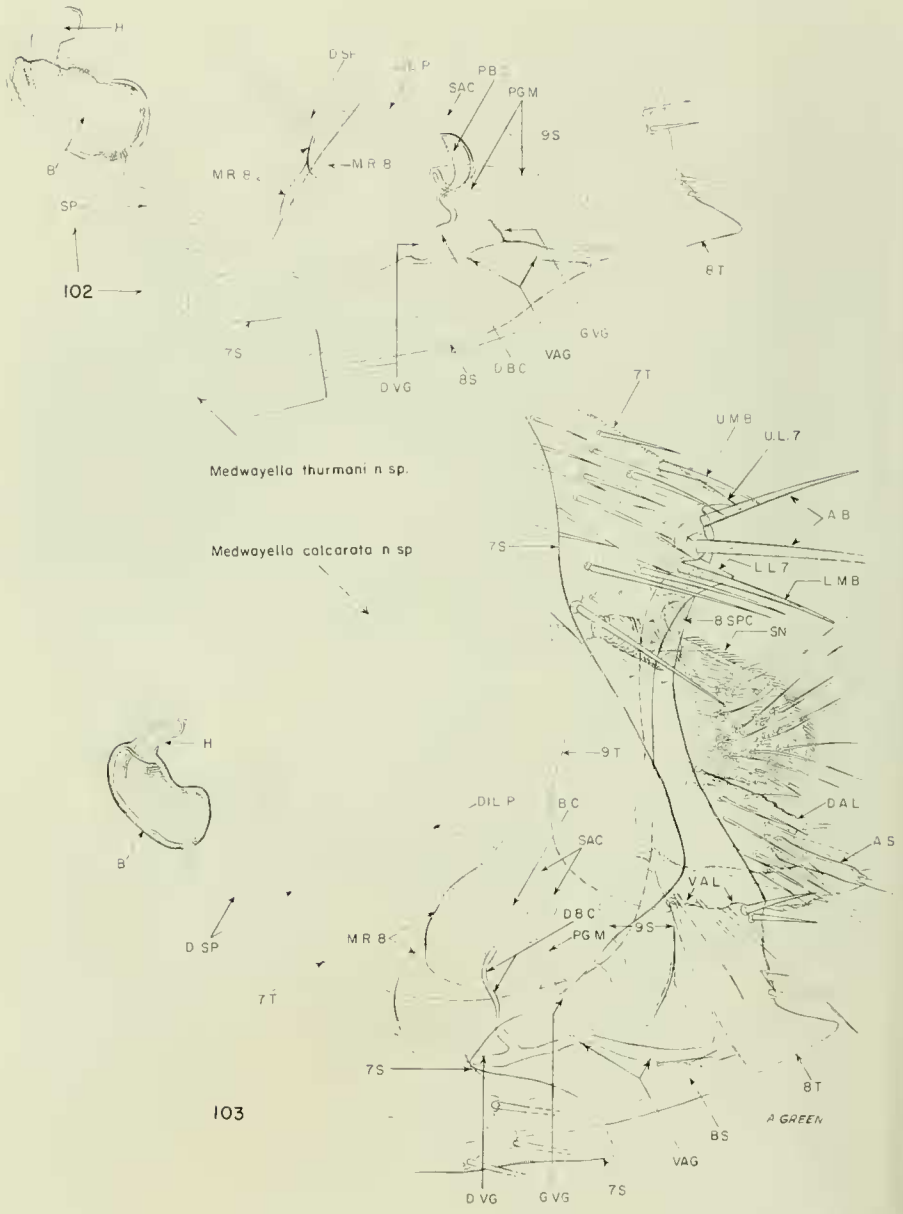
FIGS. 95-96
M. JAVANA
(JORDAN, 1933)

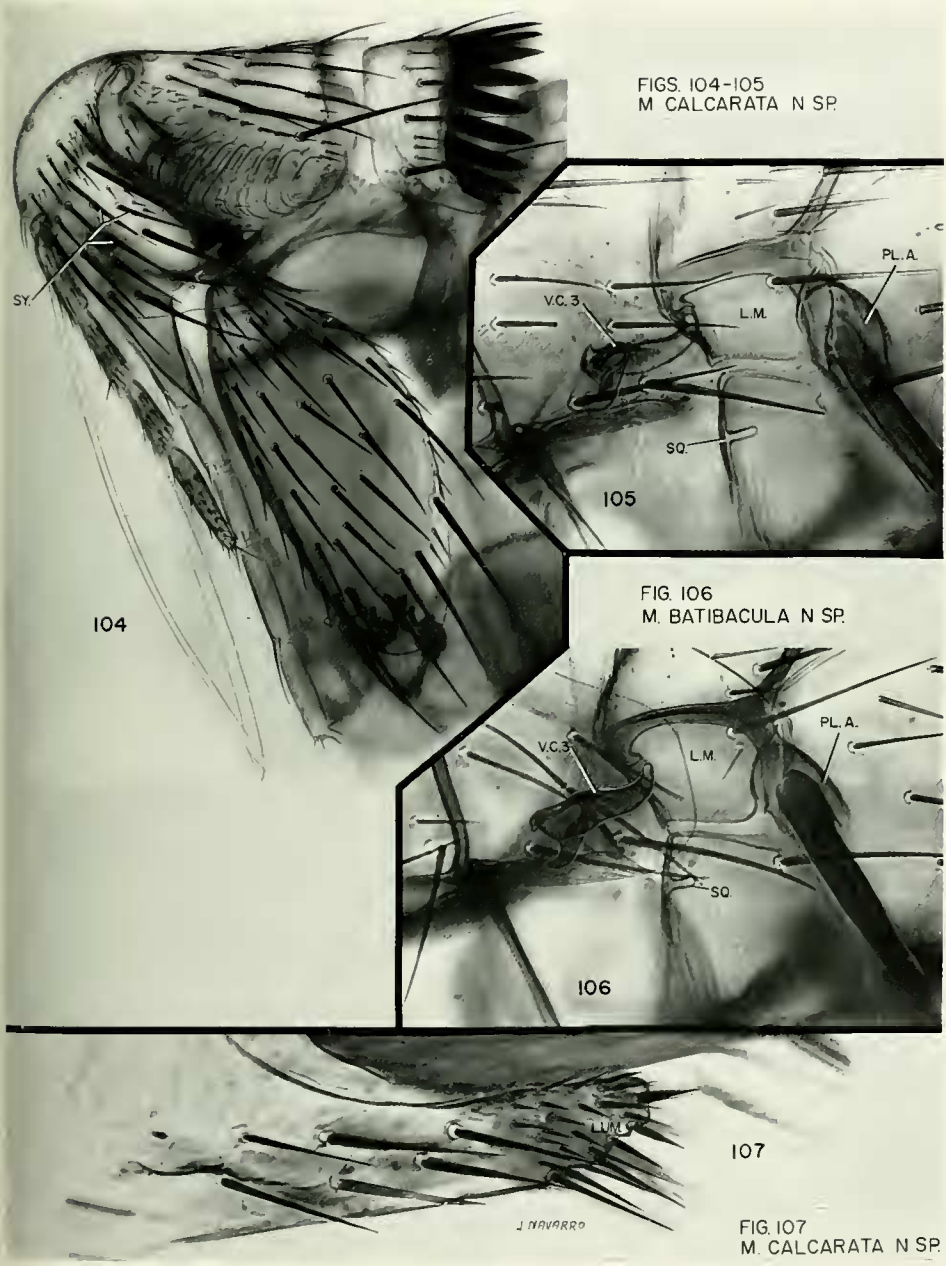
FIG. 93
M. DRYADOSA N.SP.

FIG. 94
M. THURMANI N.SP.


ALPH
MDL
BCR
THM
M thurmani n sp
PIVR
DEL FL
HD
SEC
TLS.
FUL ML
LSC
CENS
CS
LSC
UA
SAT.S.
PIV CD.
L A
FUL L L
S.I.T
CR P
PR
DV
YS.
VV
V
Q C
97
DEL FL.
AE P-V
AE P-L.
S I T
L L
PHY
THM
ALPH
BCR
PIVR.
DEL FL
HD.
FUL ML
CEN S.
TLS.
LSC.
CS.
LSC
UA
SAT S
PIV CD.
L.A
B CR.
S I T
CR P
98
S.I.T
Q C
DV
PR
YS
VV
V
M arcuata n s.
FUL. L L
AE P-V
AE P-L
L L
PHY.
AE P-L
DEL FL


FIGS. 99–101
M. THURMANI N SP.
A.B.
L.L.7
7 SPC.
L.M.B.
L.M.B. 2
7T
7S.
SP.
M.R.8
99
L.M.
VC. 3
SQ.
100
l3
l3
h3
k3
m3
SU. 8
l 3
n3
o3
f3
LUM.
s3
q3
r3
p3
101
J. NAVARRO

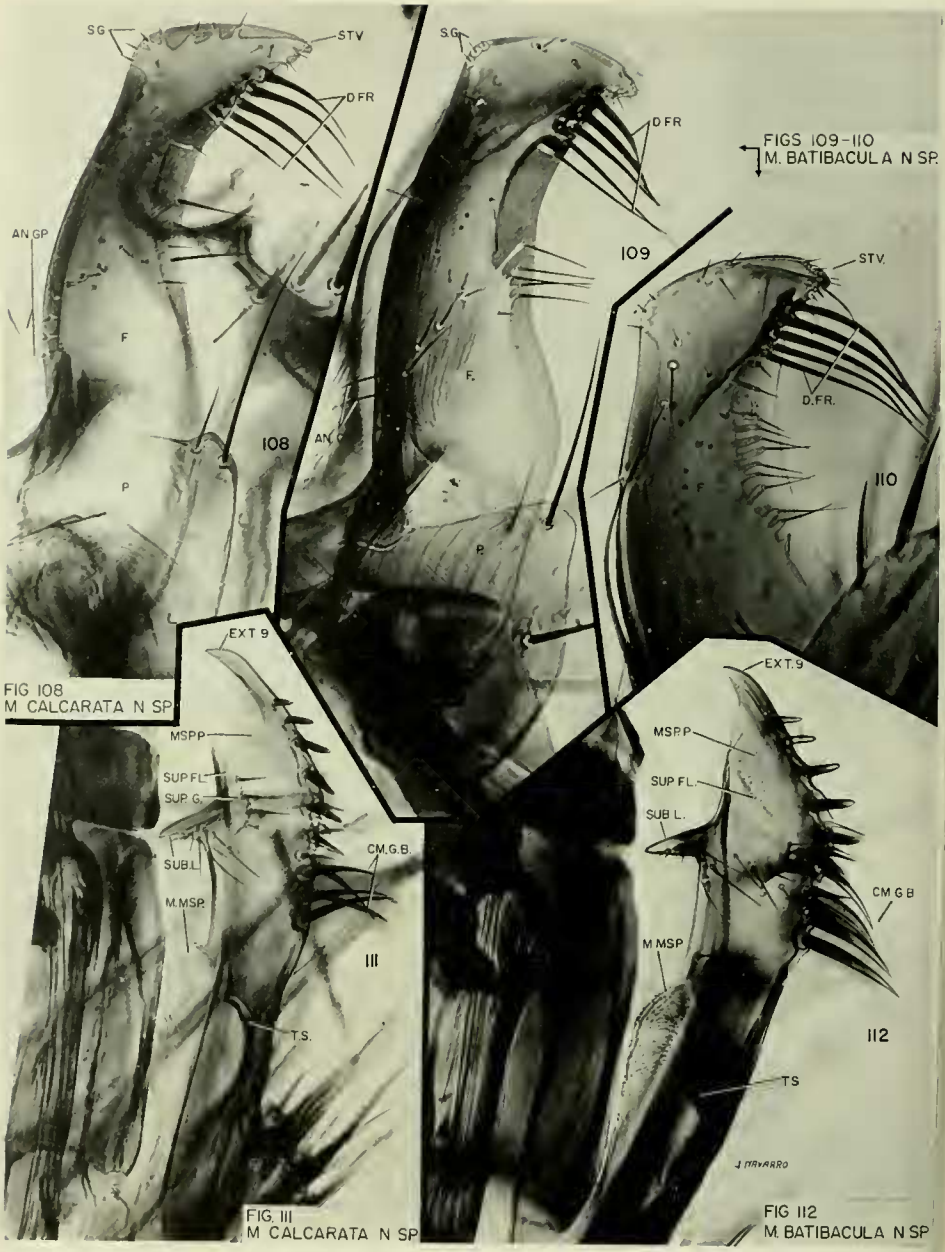

H
B'
SP
102
D SP
L P
PB
SAC
PGM
9S
MR 8
MR 8
8T
7S
DVG
8S
DBC
VAG
GVG
7T
UMB
U.L.7
Medwayella thurmani n sp.
Medwayella calcarata n sp
A B
7S
LL7
LMB
8SPC
SN
H
B'
9T
DIL P
BC
DAL
SAC
A S
VAL
DBC
PGM
9S
D SP
MR 8
7T
7S
8T
103
BS
A GREEN
VAG
DVG
GVG
7S



FIGS. 104–105
M. CALCARATA N SP.

FIG. 106
M. BATIBACULA N SP.

FIG. 107
M. CALCARATA N SP.


SG
STV
D FR
AN GP
F
P
108
FIG 108
M CALCARATA N SP
S.G.
D FR
FIGS 109-110
M. BATIBACULA N SP.
109
STV.
D.FR.
110
EXT 9
MSPP
SUP FL
SUP G.
SUB L
M.MSP.
CM.G.B.
III
T.S.
FIG. III
M CALCARATA N SP
EXT.9
MSPP
SUP FL.
SUB L.
CM G B
M MSP
112
TS
J. NAVARRO
FIG 112
M. BATIBACULA N SP

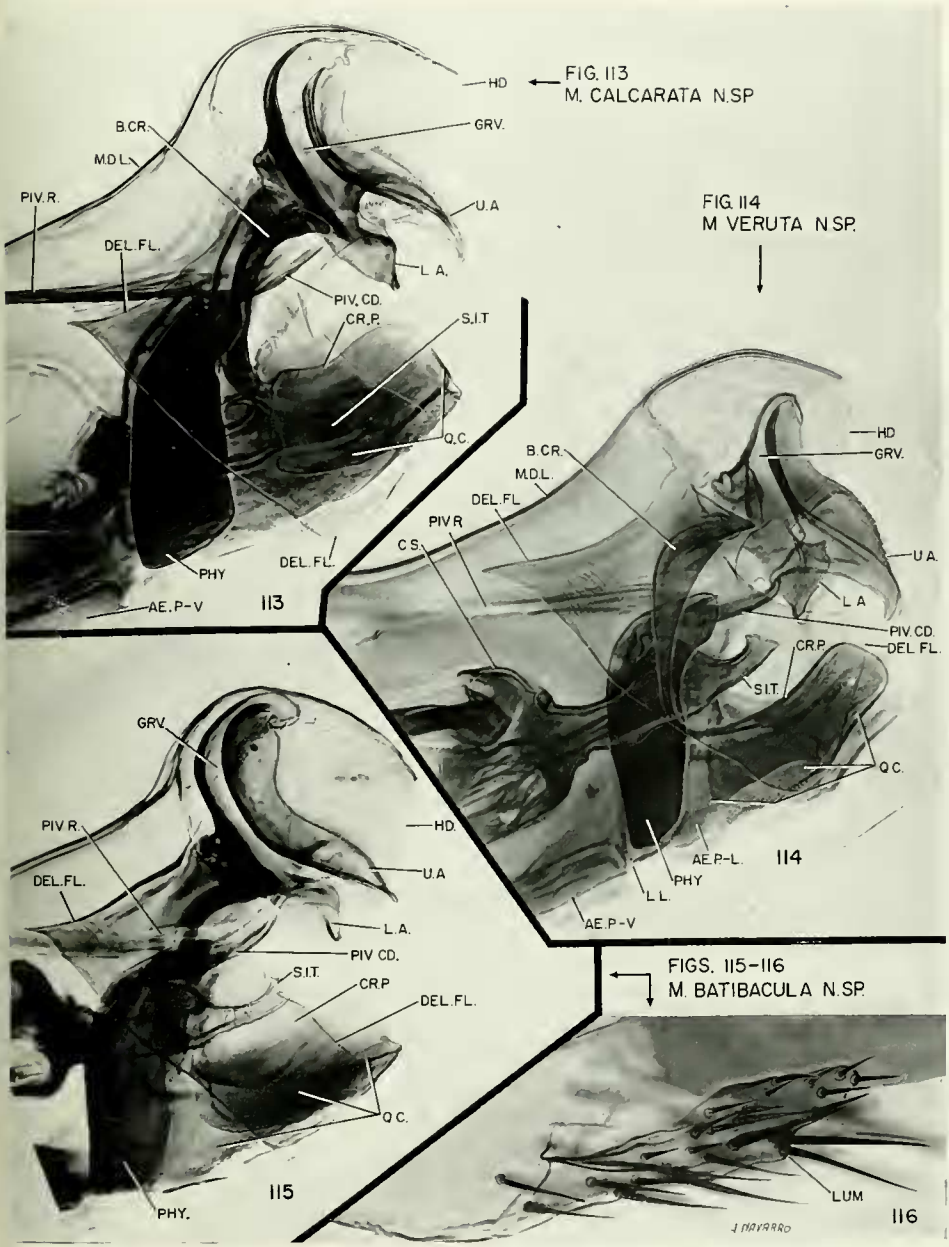
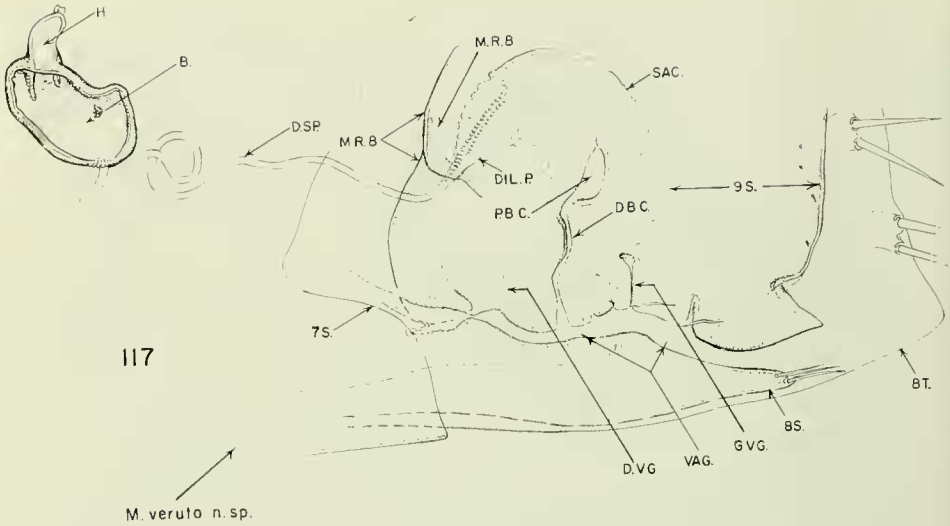
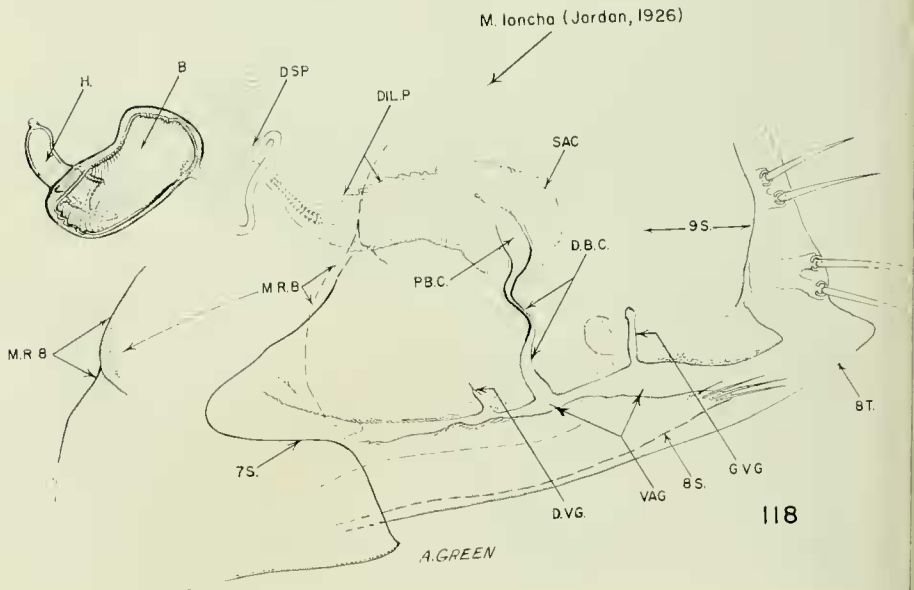


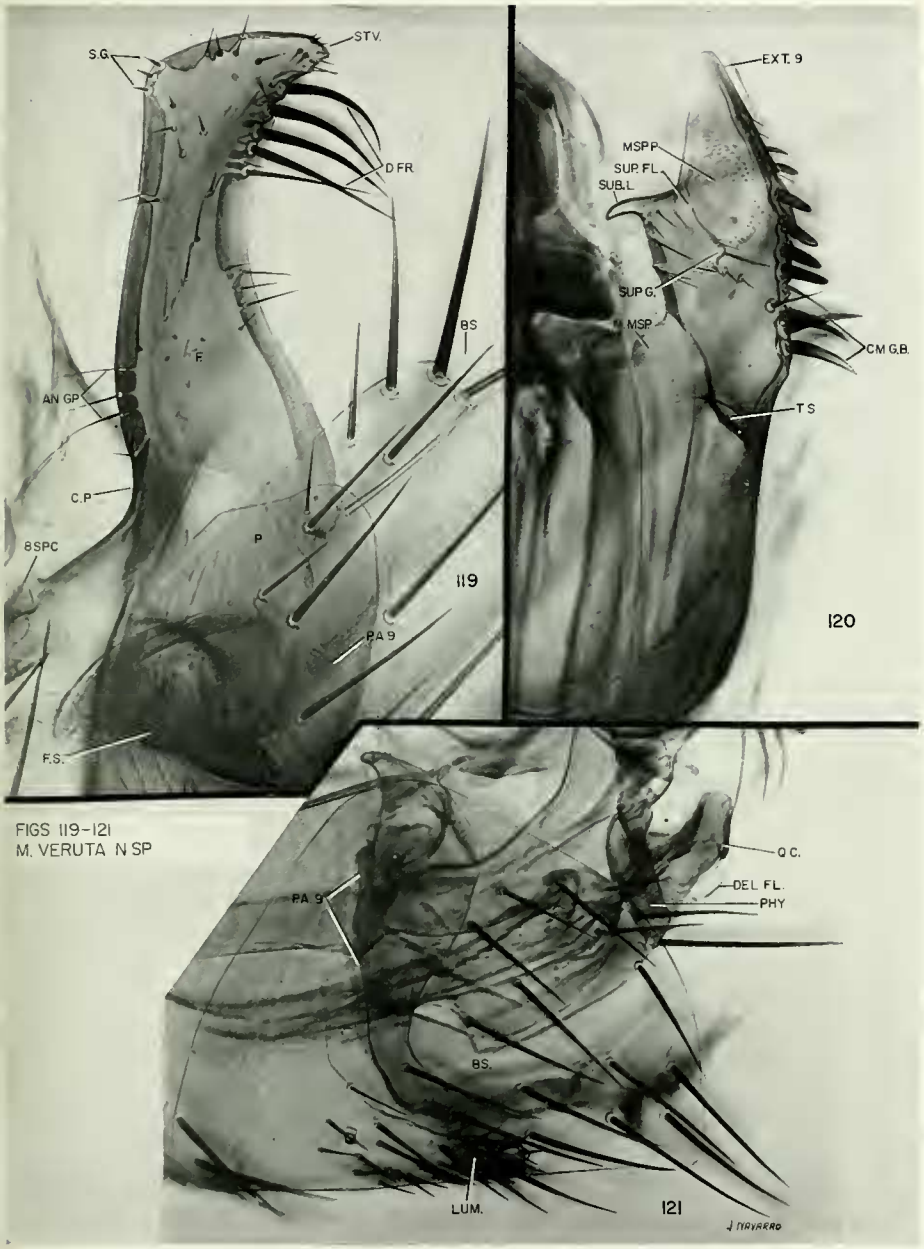
FIG. 113
M. CALCARATA N.SP
FIG. 114
M VERUTA N.SP.
FIGS. 115-116
M. BATIBACULA N.SP.
HD
GRV.
B.CR.
M.D.L.
PIV.R.
U.A
DEL. FL.
L. A.
PIV. CD.
CR.P.
S.I.T
Q.C.
PHY
DEL. FL.
AE.P-V
113
B.CR.
HD
GRV.
M.D.L.
DEL. FL.
PIV R
C.S.
U.A
L.A
PIV. CD.
CR.P.
DEL. FL.
S.I.T.
Q.C.
AE.P-L.
114
PHY
L.L.
AE.P-V
GRV.
PIV R.
HD.
U.A
DEL.FL.
L.A.
PIV CD.
S.I.T.
CR.P
DEL.FL.
Q.C.
PHY.
115
LUM
116
J. NAVARRO


H
B.
M.R.B
SAC.
D.SP.
M.R.B
DIL.P
9S.
P.B.C.
D.B.C.
7S.
8T.
8S.
G.V.G.
D.VG
VAG.
M. veruto n. sp.

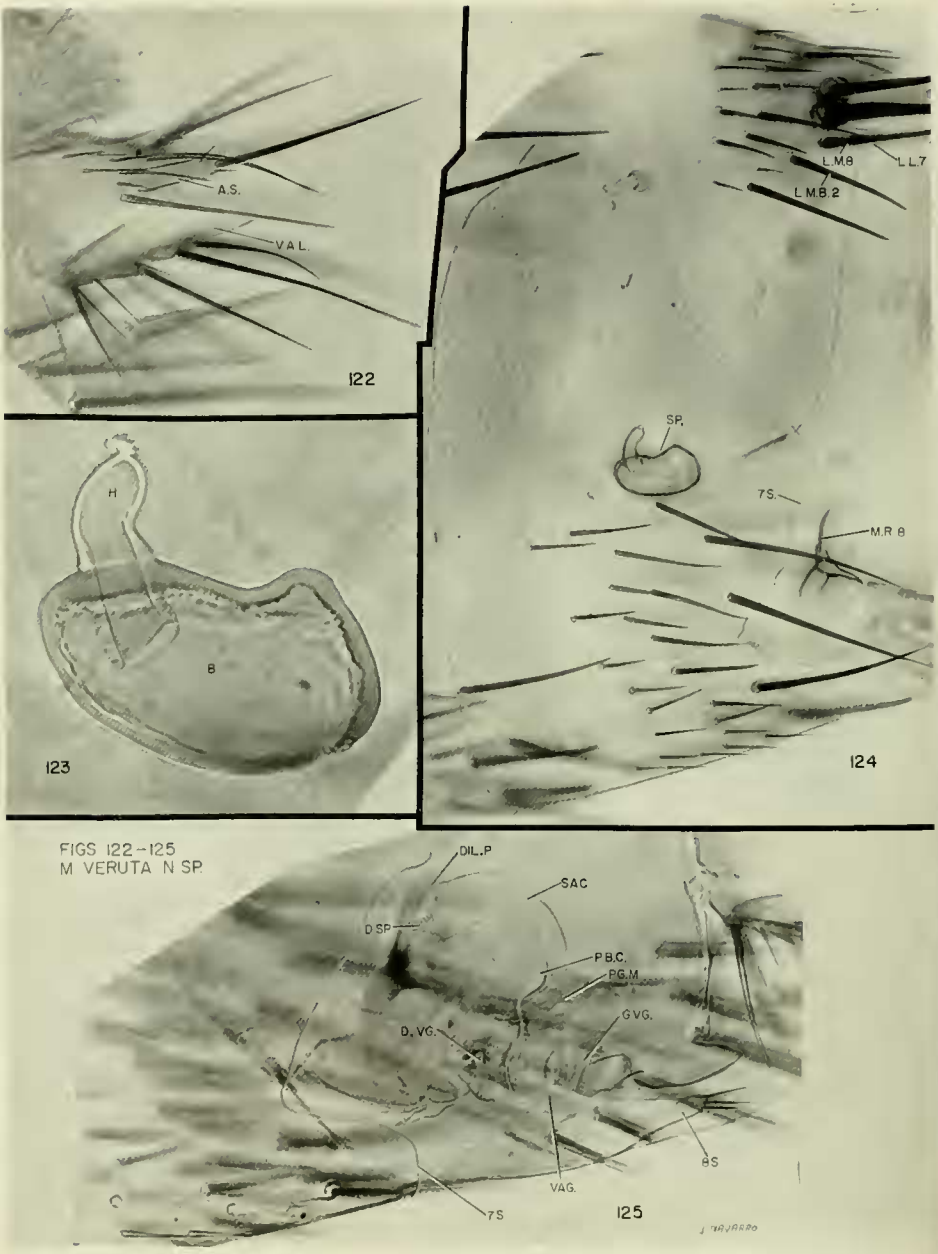
117


M. loncha (Jordan, 1926)
H.
B
D.SP
DIL.P
SAC
9S.
D.B.C.
P.B.C.
M.R.B
M.R.B
8T.
7S.
8S.
G.V.G
VAG
D.VG.
A.GREEN

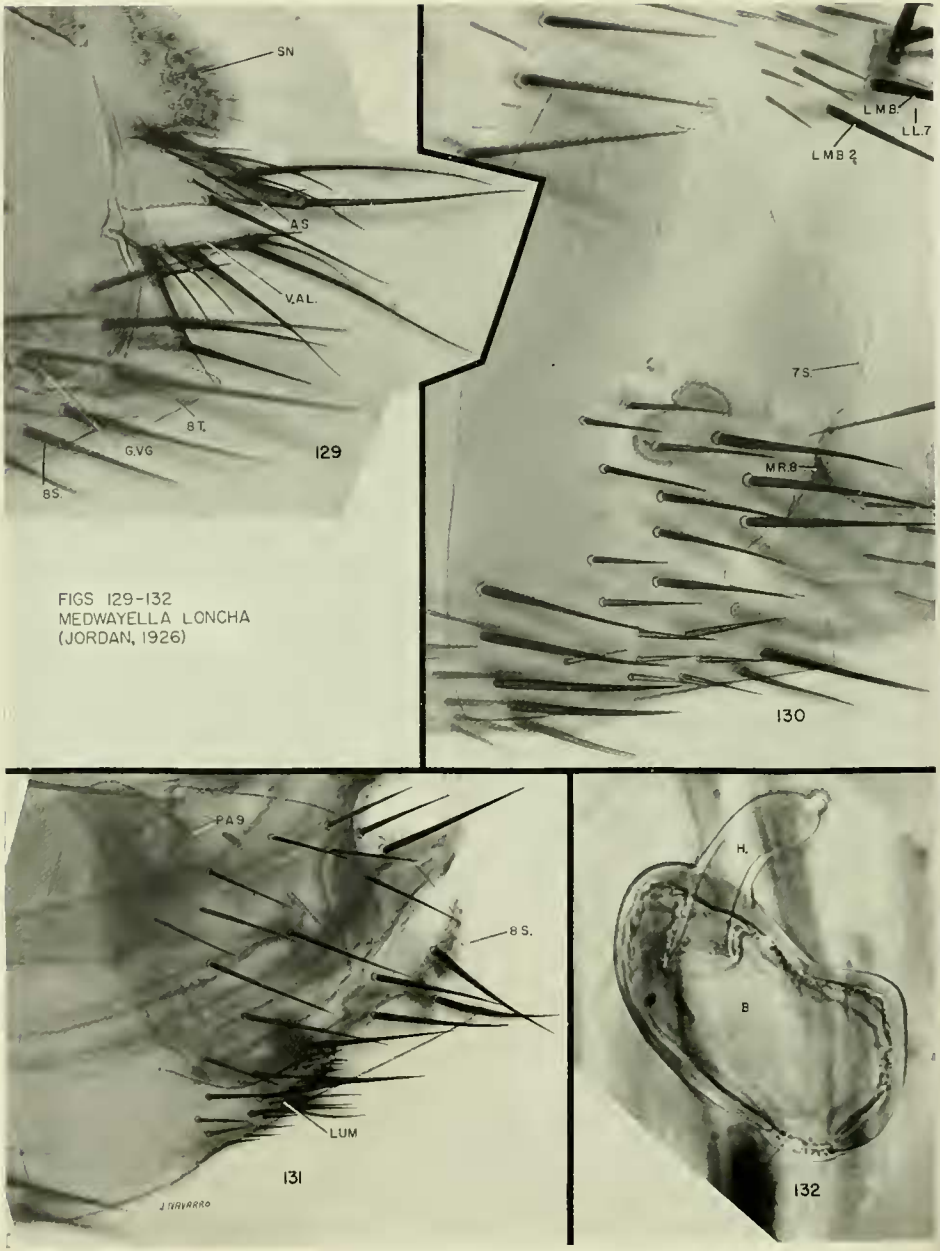
118



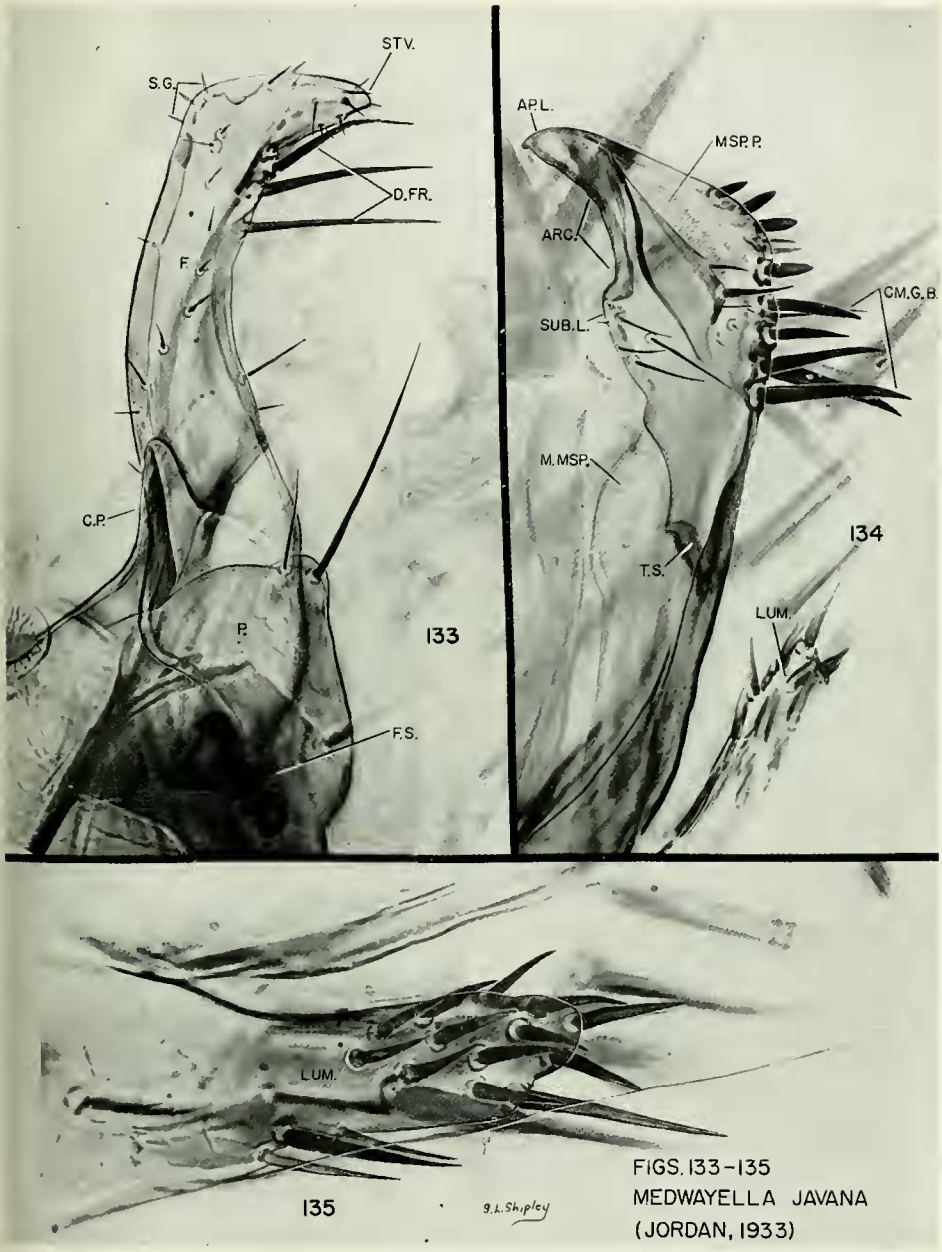
FIGS 119–121
M. VERUTA N SP


A.S.
V.A.L.
122
L.M.8
L.L.7
L.M.8.2
SP.
7S.
M.R.8
124
H
B
123
FIGS 122–125
M. VERUTA N.SP.
DIL.P
SAC.
D.SP.
P.B.C.
P.G.M.
G.V.G.
D.V.G.
8S
VAG.
7S
125

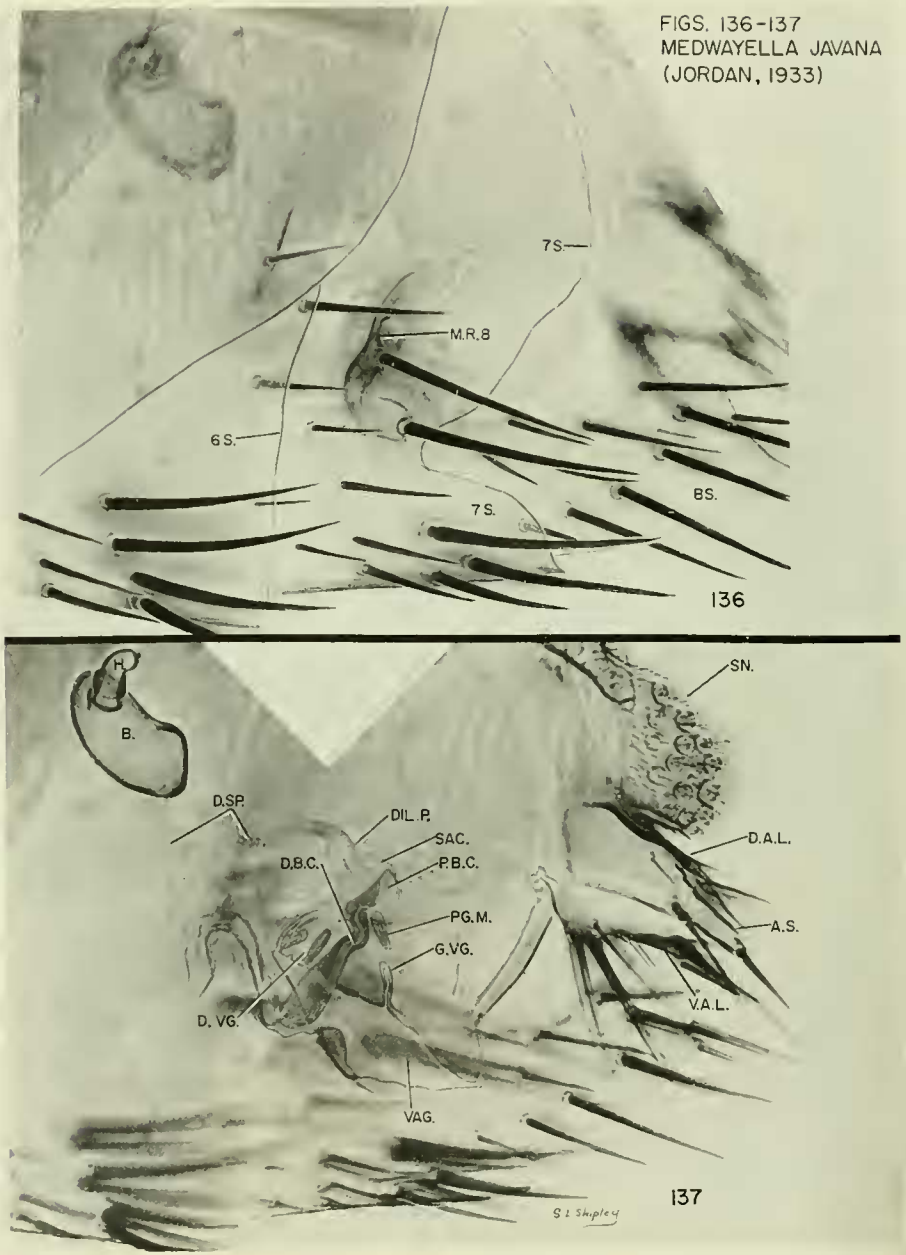
FIGS. 126–128
M. LONCHA
(JORDAN, 1926)



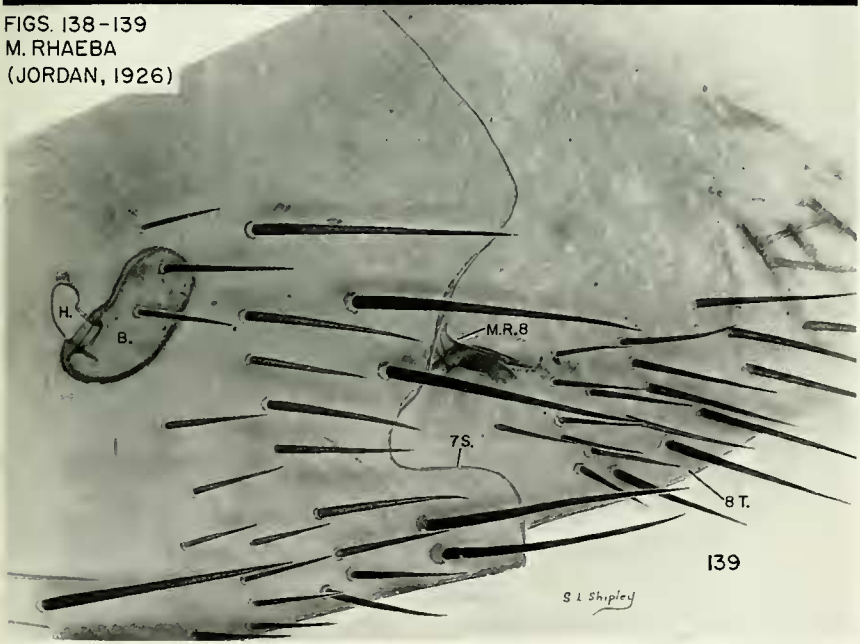
FIGS 129–132
MEDWAYELLA LONCHA
(JORDAN, 1926)

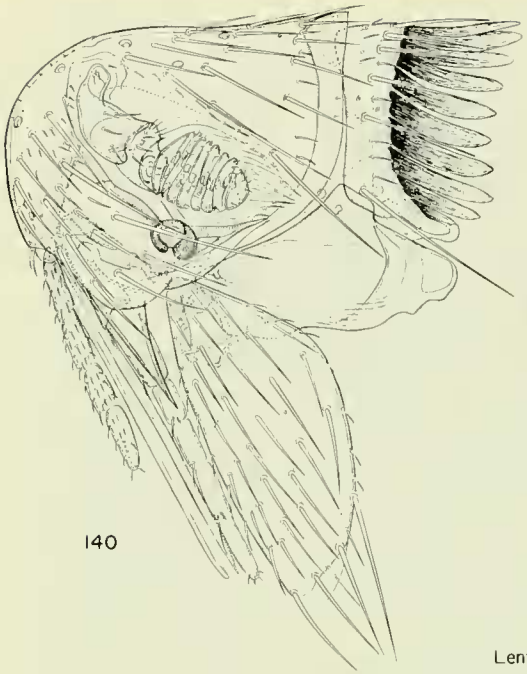


FIGS. 133–135
MEDWAYELLA JAVANA
(JORDAN, 1933)

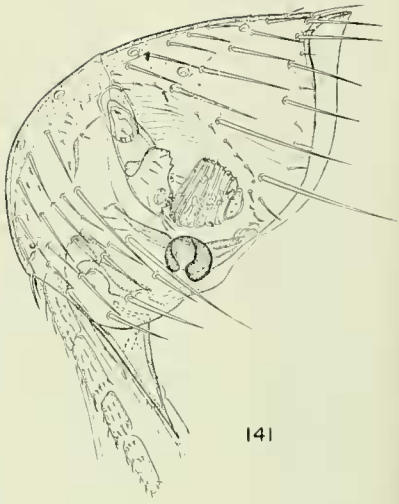

FIGS. 136-137
MEDWAYELLA JAVANA
(JORDAN, 1933)
7S
M.R.8
6S.
7S.
BS.
136
H.
B.
SN.
D.SP.
DIL. P.
SAC.
D.A.L.
D.B.C.
P.B.C.
PG.M.
A.S.
G.VG.
V.A.L.
D. VG.
VAG.
S. I. Shipley
137

FIGS. 138–139
M. RHAEBA
(JORDAN, 1926)



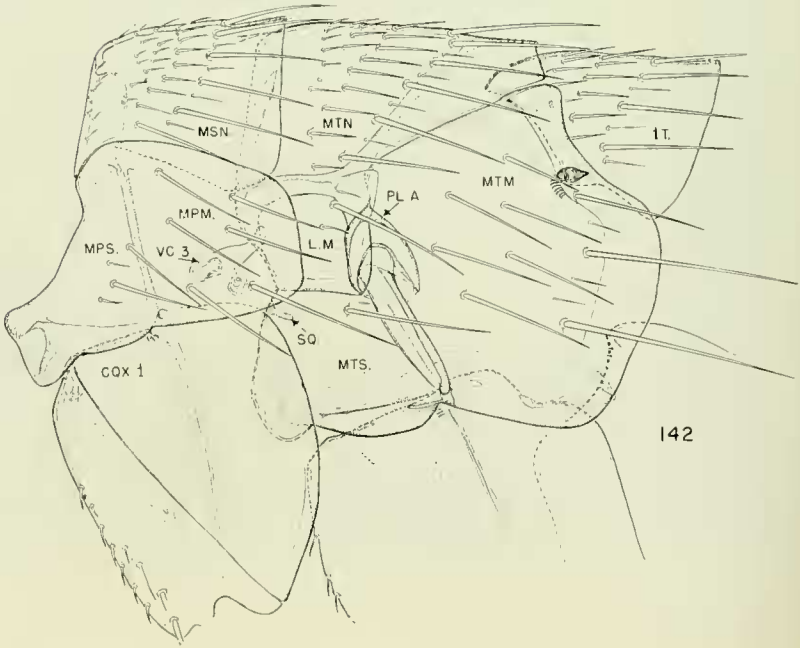


140

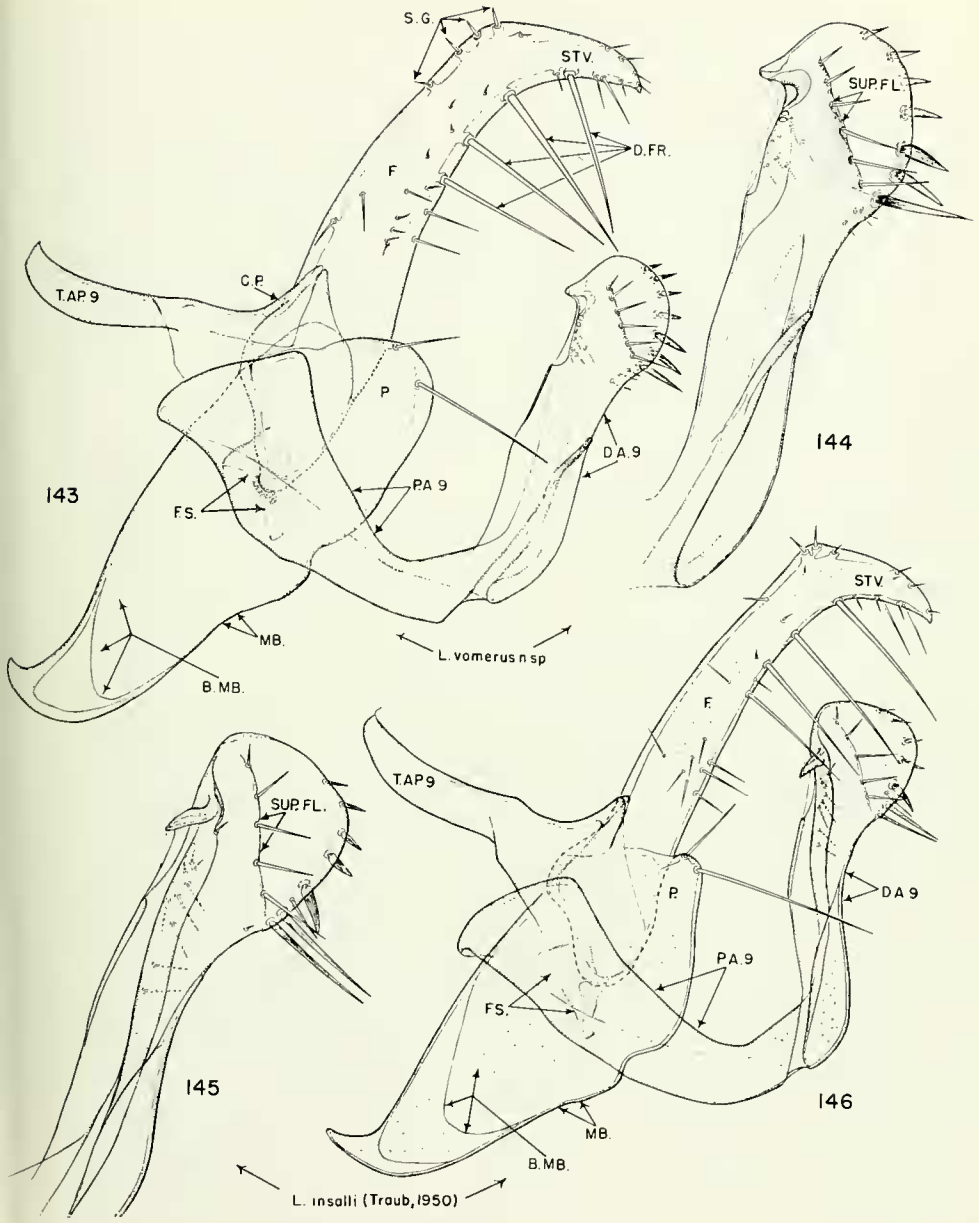


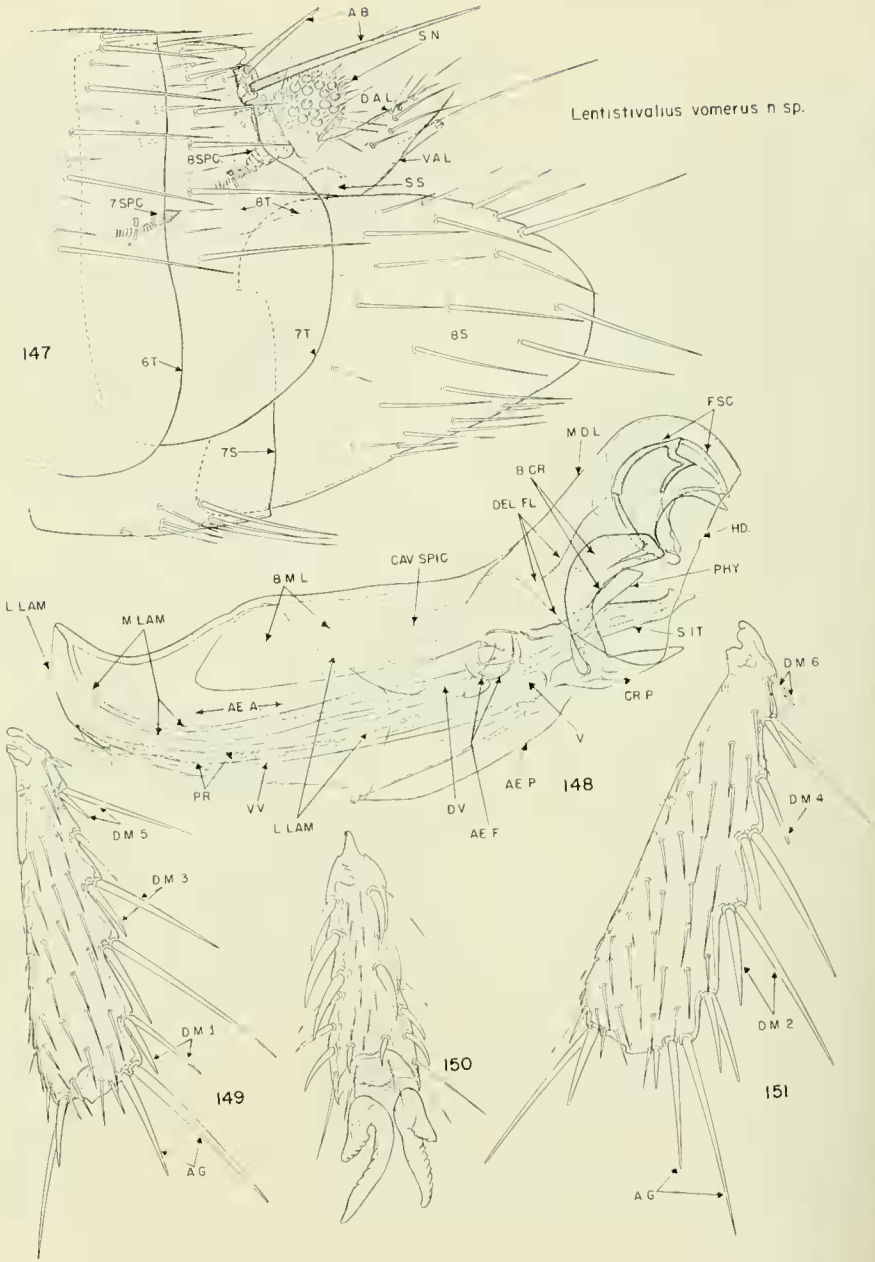
141

Lentistivalius vomerus n. sp.

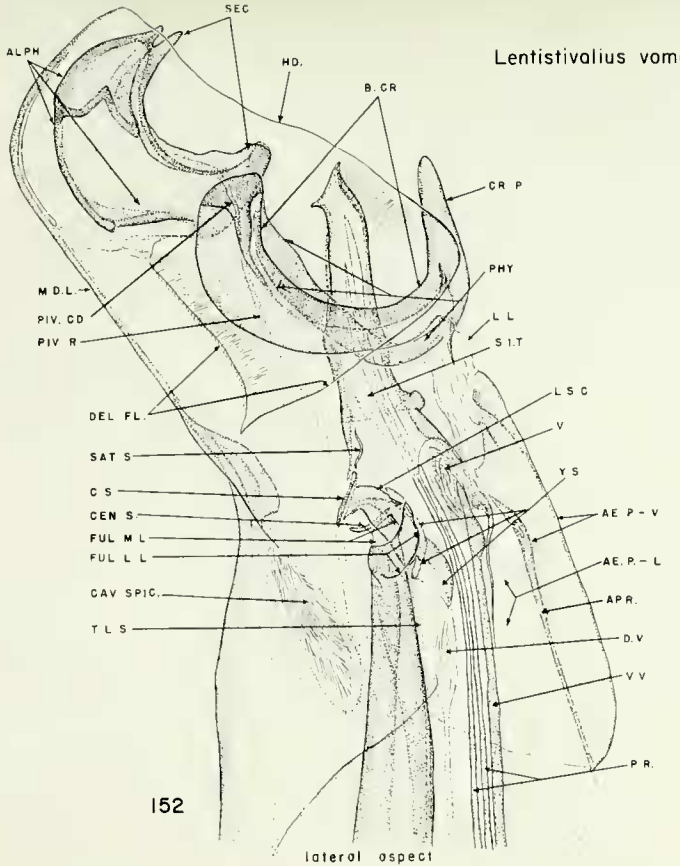


142


S.G.
STV.
D.FR.
F
C.P.
T.AP.9
P
D.A.9
143
F.S.
PA.9
MB.
B.MB.
L. vomerus n.sp
144
SUP.FL.
STV.
F
T.AP.9
P
D.A.9
PA.9
F.S.
MB.
B.MB.
146
SUP.FL.
145
L. insalli (Traub, 1950)

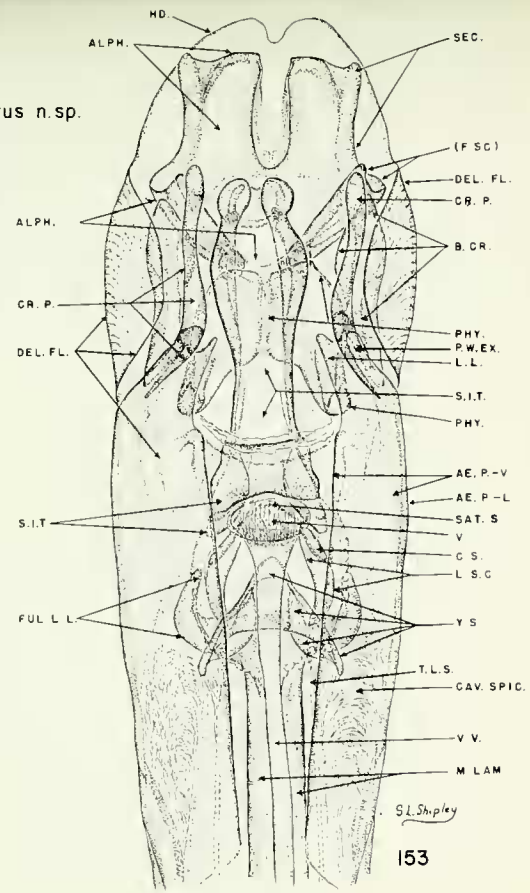

Lentistivalius vomerus n sp.
AB
SN
DAL
VAL
SS
8SPC
7SPC
8T
7T
8S
6T
7S
147
FSC
MDL
BCR
DEL FL
HD.
PHY
SIT
CRP
CAV SPIC
8ML
L LAM
M LAM
AE A
PR
VV
L LAM
DV
AE F
AE P
V
148
DM 6
DM 4
DM 2
DM 5
DM 3
DM 1
AG
149
150
151
AG

Lentistivalius vomerus n. sp.



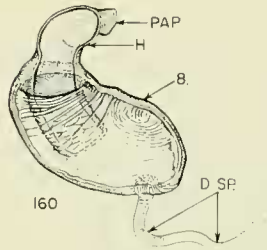
152

lateral aspect

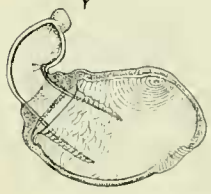


153

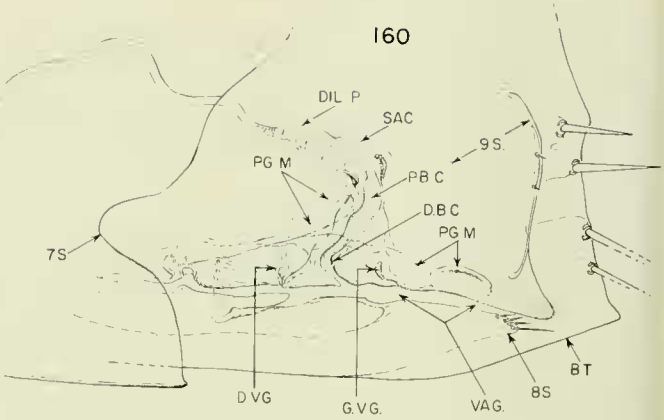
ventral aspect



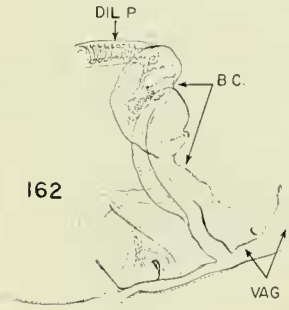
L. vomerus n. sp.

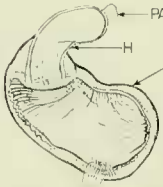


variation (aspect)

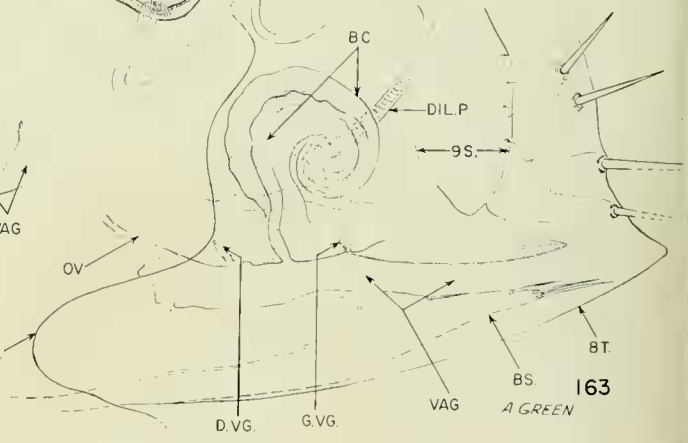


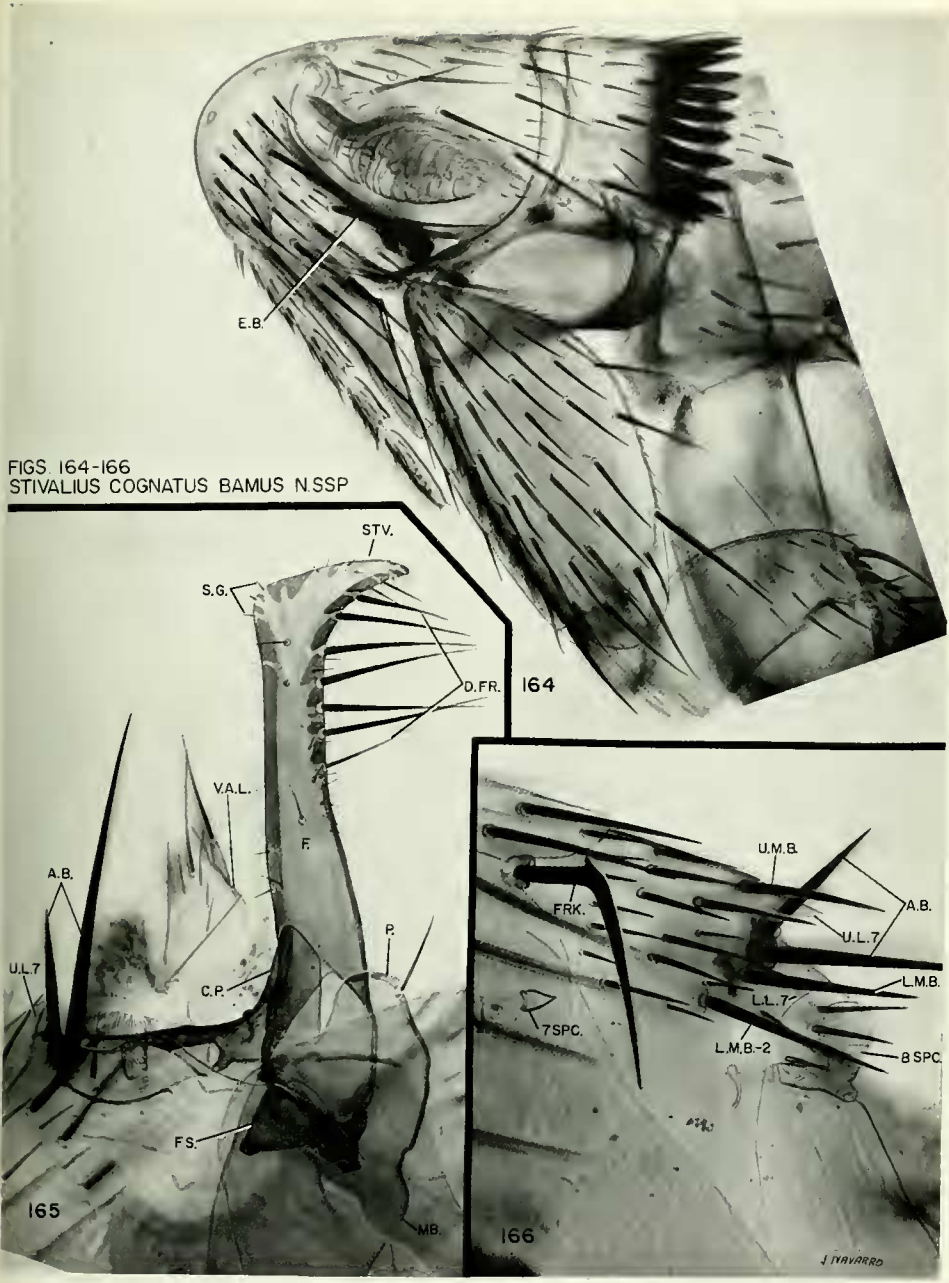
S. phoberus Jordan & Rothschild, 1922





S. cognatus bamus n. ssp.




E.B.
FIGS. 164-166
STIVALIUS COGNATUS BAMUS N.SSP
STV.
S.G.
D.FR.
164
V.A.L.
F.
A.B.
U.L.7
C.P.
P.
FS.
MB.
165
U.M.B.
FRK.
A.B.
U.L.7
L.M.B.
L.L.7
7SPC.
L.M.B.-2
8 SPC.
166
J. TAVARRO

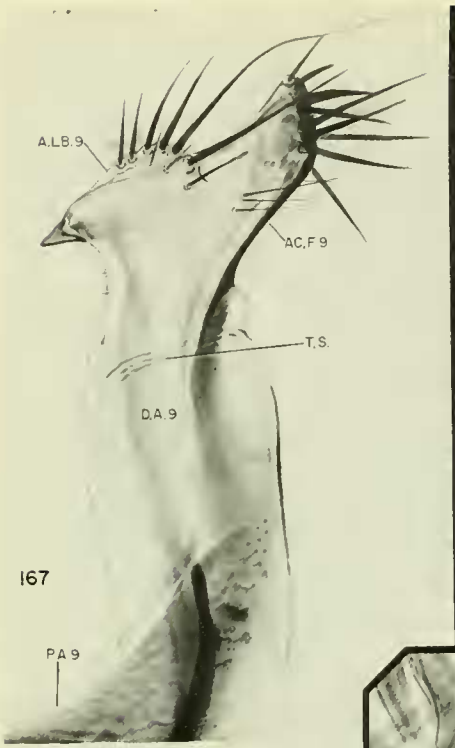


FIG. 167
STIVALIUS COGNATUS BAMUS N SSP

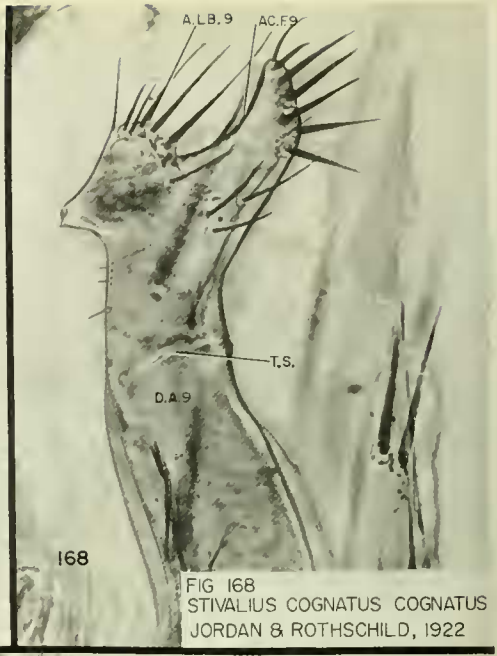


FIG 168
STIVALIUS COGNATUS COGNATUS
JORDAN & ROTHSCHILD, 1922

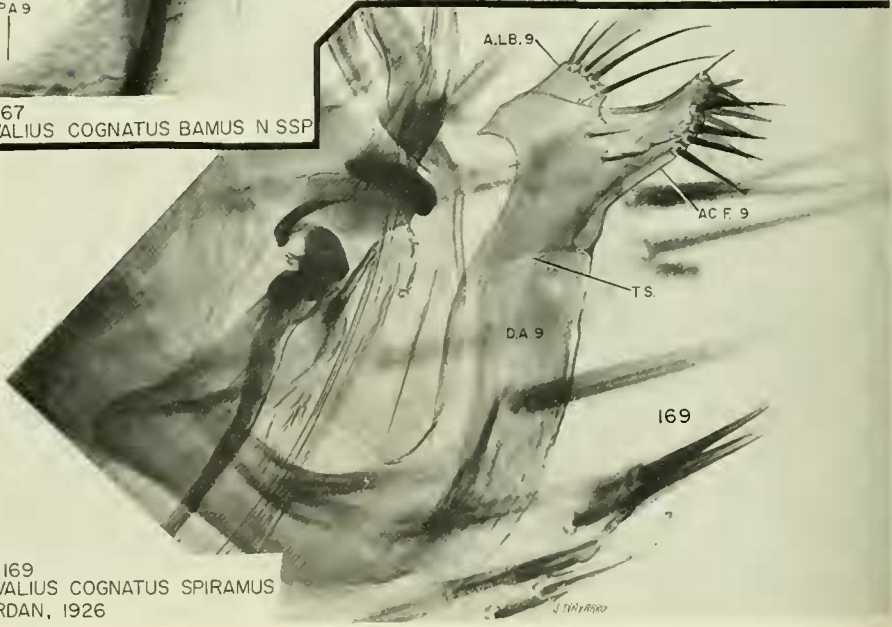
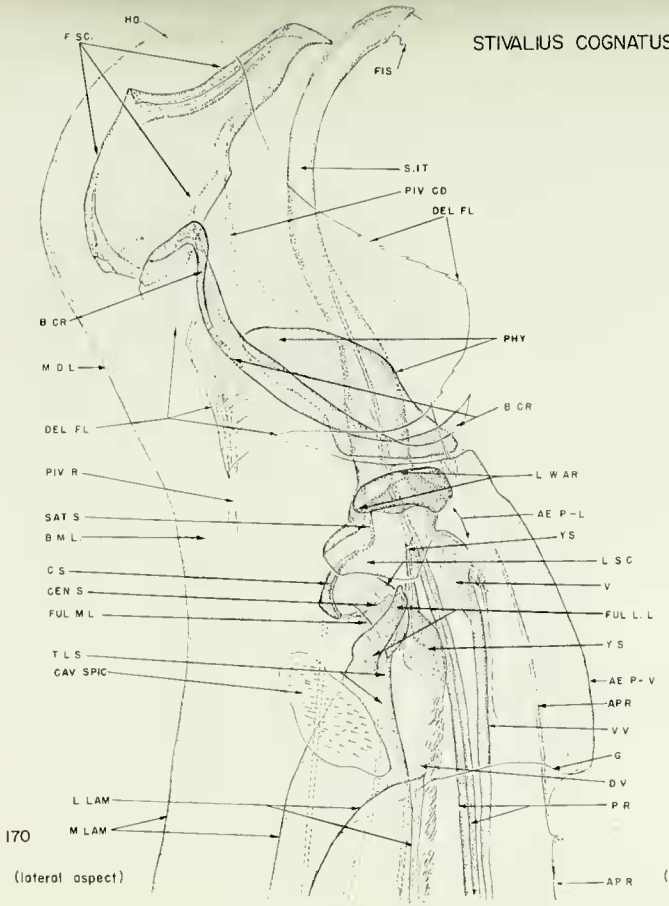


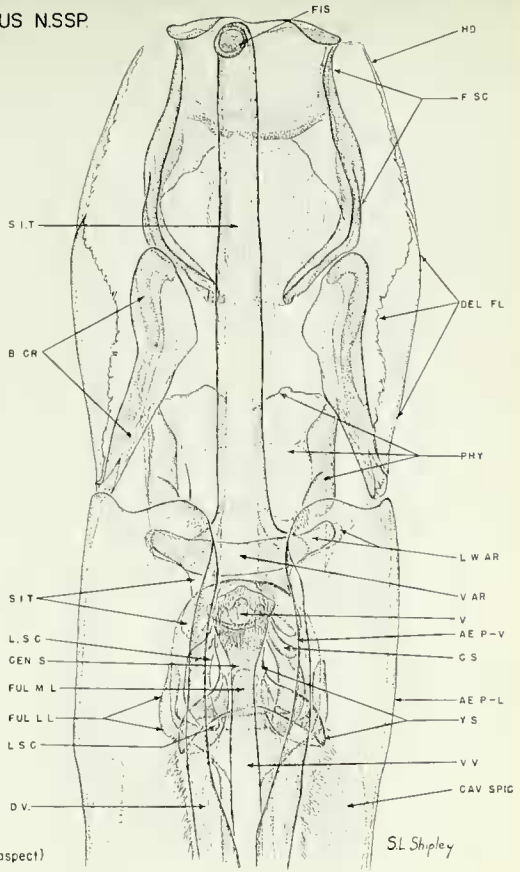
FIG 169
STIVALIUS COGNATUS SPIRAMUS
JORDAN, 1926

STIVALIUS COGNATUS BAMUS N.SSP.



170

(lateral aspect)



171

(ventral aspect)

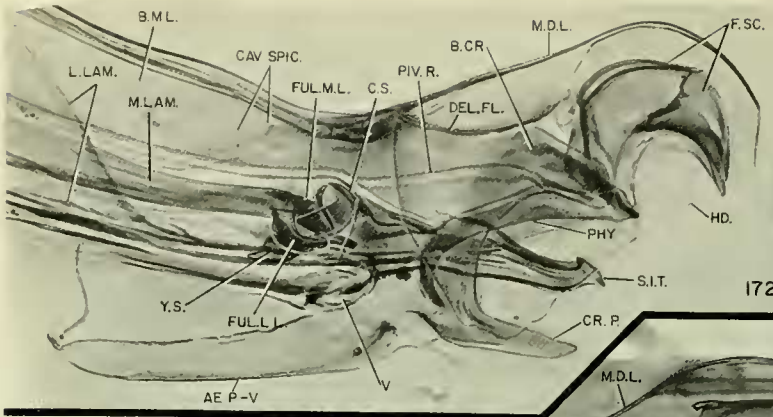


FIG 172
LENTISTIVALIUS
VOMERUS N SP.

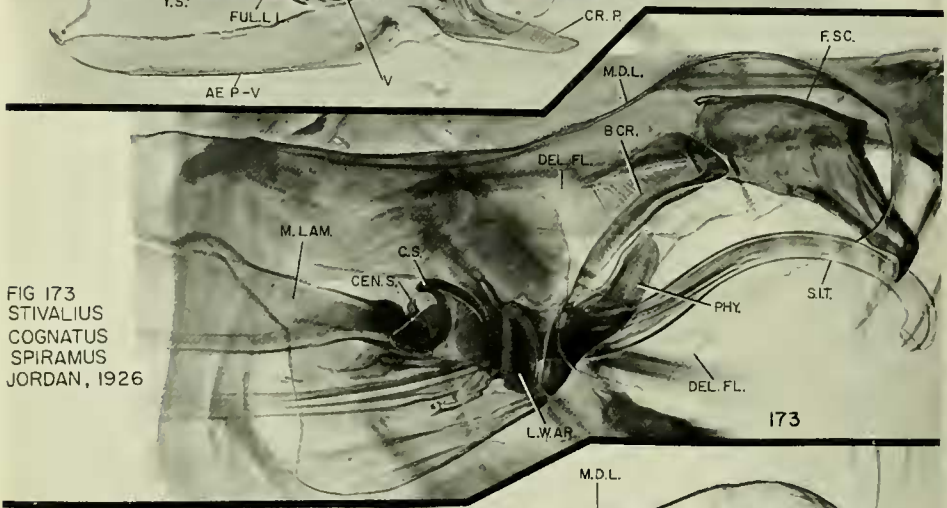


FIG 173
STIVALIUS
COGNATUS
SPIRAMUS
JORDAN, 1926

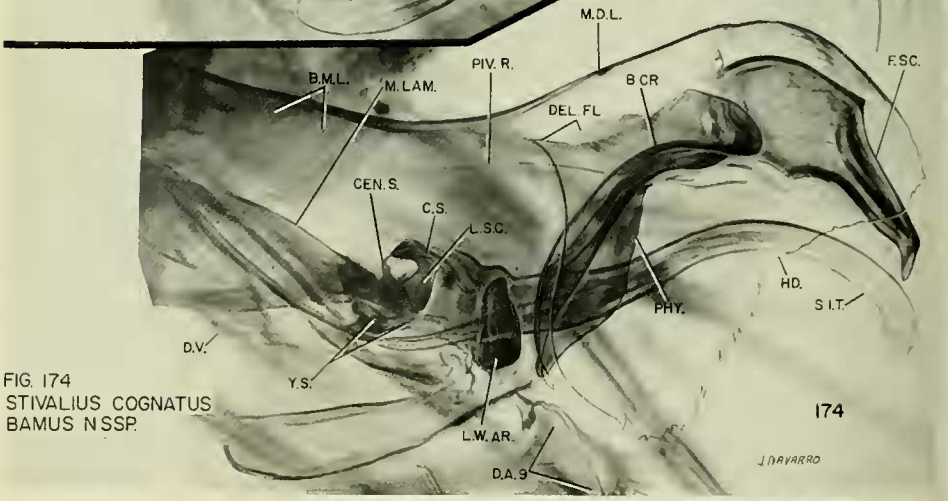
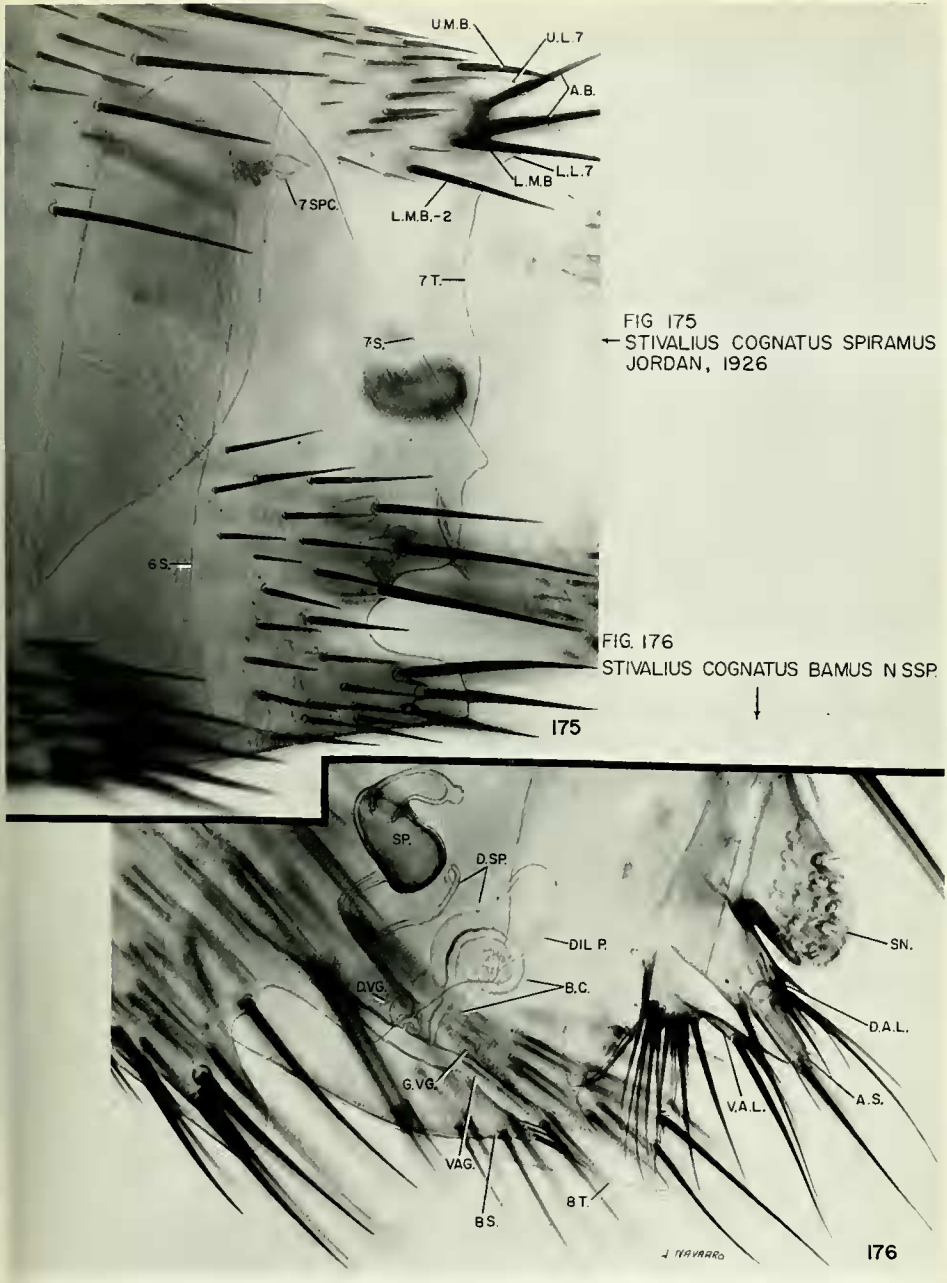


FIG. 174
STIVALIUS COGNATUS
BAMUS N SSP.


U.M.B.
U.L.7
A.B.
L.L.7
L.M.B
L.M.B.-2
7 SPC.
7 T.
7 S.
6 S.
175
FIG 175
← STIVALIUS COGNATUS SPIRAMUS
JORDAN, 1926
FIG. 176
STIVALIUS COGNATUS BAMUS N SSP.
SP.
D.SP.
DIL P.
SN.
D.VG.
B.C.
D.A.L.
G.VG.
V.A.L.
A.S.
VAG.
8 T.
8 S.
J. NAVARRO
176

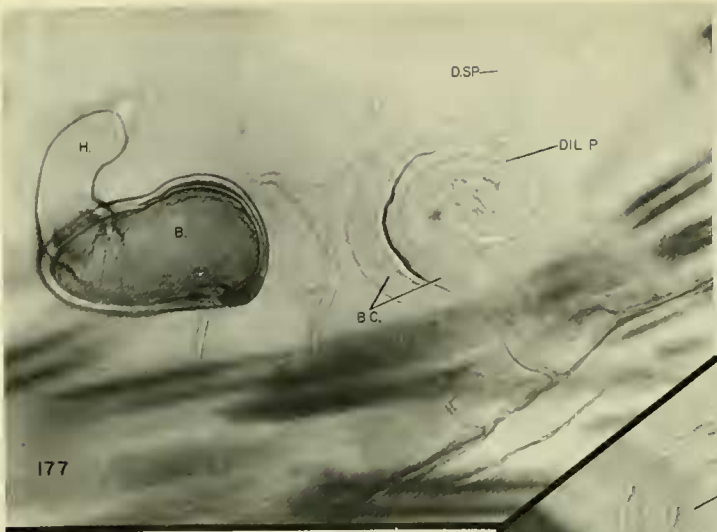


FIG 177 ↑
STIVALIUS COGNATUS BAMUS N SSP

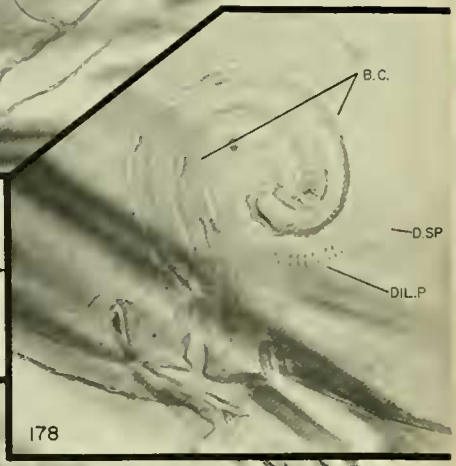


FIG. 178
STIVALIUS COGNATUS SPIRAMUS →
JORDAN, 1926

FIG. 179
STIVALIUS COGNATUS COGNATUS ↰
JORDAN & ROTHSCHILD, 1922